BREEDING ECOLOGY, SOCIAL ORGANIZATION AND COMMUNICATORY BEHAVIOUR OF THE BROWN CREEPER (*FINSCHIA NOVAESEELANDIAE*)

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ABSTRACT

The breeding ecology, social organization and communicatory behaviour of the brown creeper (Finschia novaeseelandiae) were studied.

Brown creepers lay large eggs, young develop slowly and incubation and nestling periods are long. Mortality in adults is low but high in juveniles. I suggest that the species' breeding strategy is an adaptation to the mild coastal climate of New Zealand.

Members of breeding pairs remain together and defend territories throughout the winter. Juveniles form sibling flocks and this association of close relatives may help explain winter mobbing behaviour in the species.

The communicatory repertoire consists of 19 vocal and seven visual displays each of which encode several messages. Graded vocal sequences are also used; conceivably because most interactions between conspecifics take place at close range.

Three stages in song ontogeny are described. Young males learn song from neighbours they interact with, not fathers. Eight song dialects were studied. The historical model best explains the origin of brown creeper dialects, whereas Payne's (1981) social adaptation hypothesis accounts for the formation and adaptive significance of subdialects.

When local and foreign dialects differed markedly, males responded more strongly to the local theme. Similar dialects received equal responses. The lower responses to a foreign dialect may be due to its dissimilarity to the local song.

Responses were greater to the songs of strangers than to neighbours. Kowhai Bush males neighbouring a male transferred from Lake Rotorua reacted more strongly to song playback from the transferred bird than did non-neighbours. The results suggest associative learning is

important in brown creeper neighbour/stranger discrimination.

An unusual vocal display (unison singing) in which two interacting males temporally overlap their songs is described. A unison singing male changes his singing pattern to that of another; such adjustments appear to allow males to define territorial boundaries.

CHAPTER 1

GENERAL INTRODUCTION

The New Zealand brown creeper or pipipi, Finschia novaeseelandiae, is a small (10.5-15.0 g; Cunningham 1984) insectivorous passerine found only on the South and Stewart Islands of New Zealand. In the Annotated Checklist of the Birds of New Zealand (OSNZ 1970), following the arrangement of Mayr and Amadon (1951), the monotypic genus Finschia is placed within the family Muscicapidae and the subfamily Malurinae (Australian Warblers). Keast (1977), however, noted that Finschia shows no obvious relationship to the Malurinae and has suggested that it is sufficiently distinct to warrant placement in a new subfamily, Mohouinae, along with the whitehead Mohoua albicilla and the yellowhead M. ochrocephala both of which are also endemic to New Zealand. Thus the brown creeper's taxonomic placement and affinities are still not well understood. The brown creeper is widespread and locally common, being found primarily in native and at times neighbouring exotic forests (Falla et al. 1979). It occurs in forests of both mature and second growth, from sea level to alpine scrub (Child 1975), possibly preferring the latter (Bull and Whitaker 1975; C.A. Fleming pers. comm.).

Although common, brown creepers have received little attention from researchers and are unknown to many of the general public. In part, this lack of attention may be due to the species' cryptic colouration and its habit of foraging and nesting in the canopy where it is difficult to be seen.

To date there has been only one major publication dealing exclusively with brown creeper biology. In this, Henderson (1977) investigated the composition and habitat utilization of brown creeper flocks in the autumn and winter. He also provided descriptions of

several of the species' vocalizations which unfortunately were neither tape recorded nor analysed sonagraphically. However Henderson's work did reveal that the vocal repertoire of the brown creeper was probably complex.

I decided to undertake a more detailed examination of the vocal repertoire of the brown creeper and attempt to understand its role in social interactions. In order to accomplish this it was also necessary to study the breeding biology of the brown creeper and its social organization during the breeding season. Furthermore, to analyse communication during the non-breeding season I had to examine the social organization of wintering birds. The singing behaviour of the brown creeper and its role in intra- and intersexual communication was also investigated by examining song variation and the responsiveness of males to this variation. While studying the singing behaviour of males, I discovered an unusual vocal display which I called unison singing. In this display, interacting neighbouring males temporally overlapped their songs, an uncommon practice among birds. I studied this behaviour in detail to attempt to understand its function in male/male communication and possible role in defining territorial boundaries.

To summarize, this study had the following objectives:

1) to describe the breeding system of the brown creeper.
2) to investigate the social organization of brown creepers in the non-breeding season.
3) to produce a catalogue of the communicatory repertoire of the species and to begin to understand its use in communication.
4) to ascertain intra individual and intra- and interpopulation variability in brown creeper song and relate this variability to theories of song learning and social organization.
5) to determine the responsiveness of breeding males to songs from different localities.

6) to investigate the ability of males to discriminate between the songs of neighbours and strangers and also determine what role associative learning may play in this discrimination.
7) to study the function of unison singing in the process of male/male communication during territorial interactions.

CHAPTER 2

STUDY AREAS

INTRODUCTION

The present study was conducted within two regions of the South Island of New Zealand: Kaikoura (173° 37' E, 42° 23' S) and Stewart Island (168° 9'E, 46° 55' S) (Fig. 2.1). Brown creeper populations at five locations near Kaikoura were studied: Kowhai Bush, West Bank, Lake Rotorua, Mount Fyffe Bush and Waimangarara River Bush (Fig. 2.2). On Stewart Island three populations were sampled: Ulva Island, Freshwater Flat, and Mason Bay Track (Fig. 2.3).

KOWHAI BUSH

Kowhai Bush is a native lowland forest 8 km northwest of Kaikoura. The forest, which is administered by the Marlborough Catchment Board, covers an area of 240 ha and lies at 60-150 m a.s.l. Kowhai Bush is bordered by farmland on the east and south, the Kowhai River on the west and connected to native forests on Mount Fyffe by a narrow corridor on the north.

The forest is a mosaic of successional stages produced by the periodic flooding of the Kowhai River. The canopy, 4-15 m high, is composed of kanuka (Leptospermum ericoides) and manuka (L. scoparium) (Gaynor 1979). Kohuha (Pittosporum tenuifolium), tarata (P. eugenioides), introduced brooms (Cytisus spp.), tutu (Coriaria arborea) and Coprosma spp. make up the understorey. (For further information on the vegetation of Kowhai Bush see Hunt and Gill (1979).

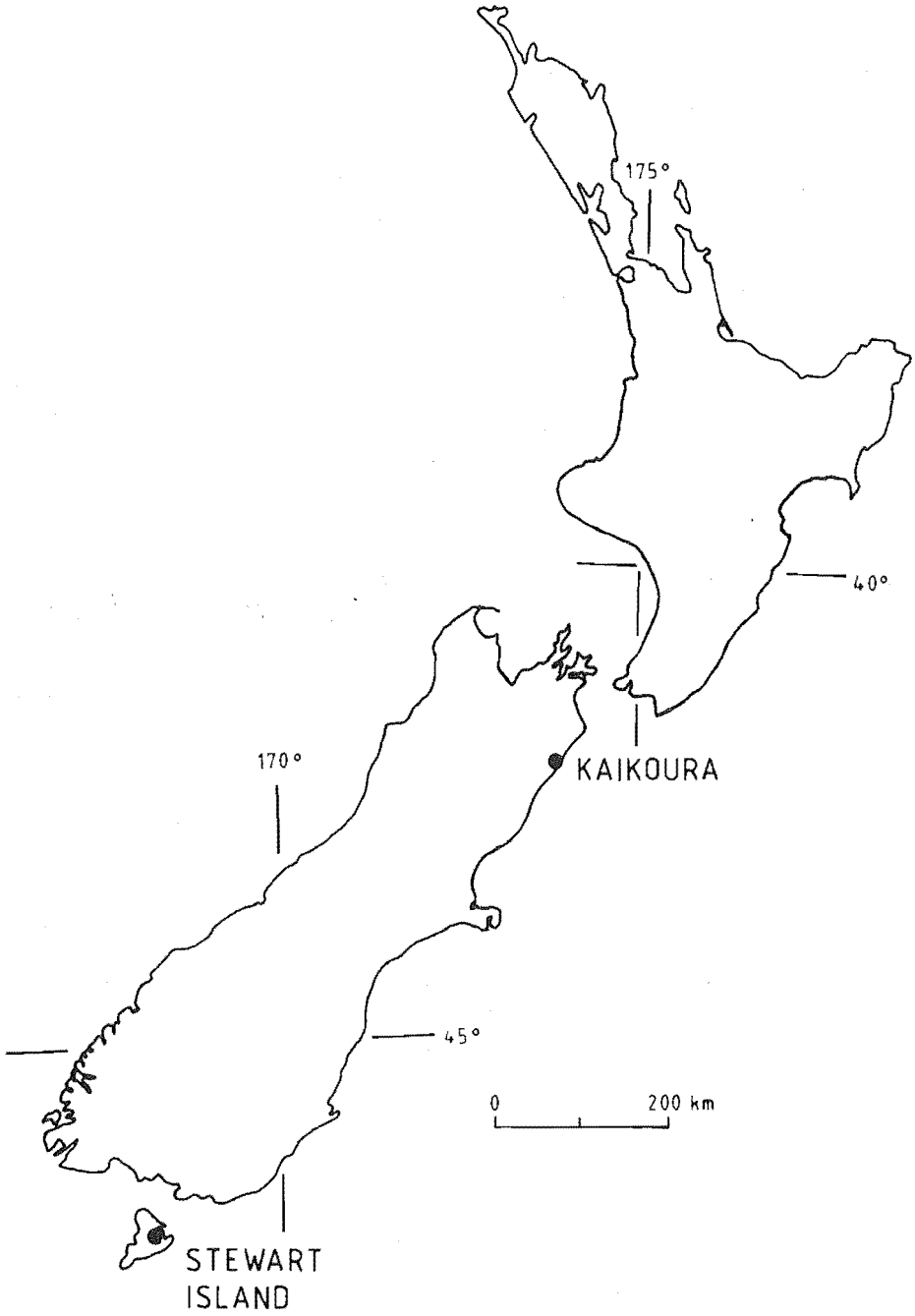

Fig. 2.1. Map of New Zealand showing the two locations where the study was conducted: Kaikoura and Stewart Island.

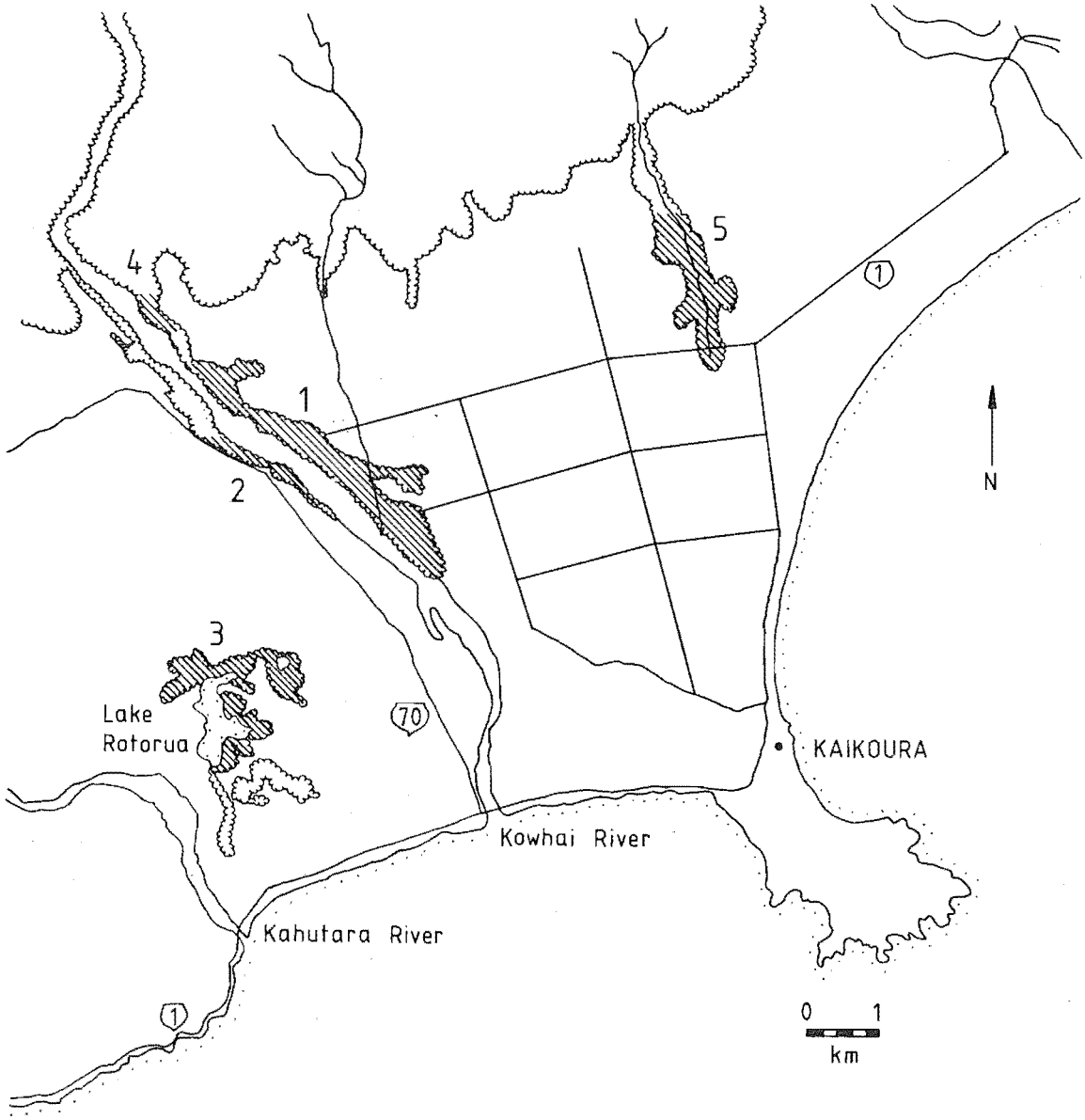

Fig. 2.2. Map of Kaikoura region. Hatched areas show localities where brown creepers were recorded. 1. Kowhai Bush, 2. West Bank, 3. Lake Rotorua, 4. Mount Fyffe, 5. Waimangarara River.

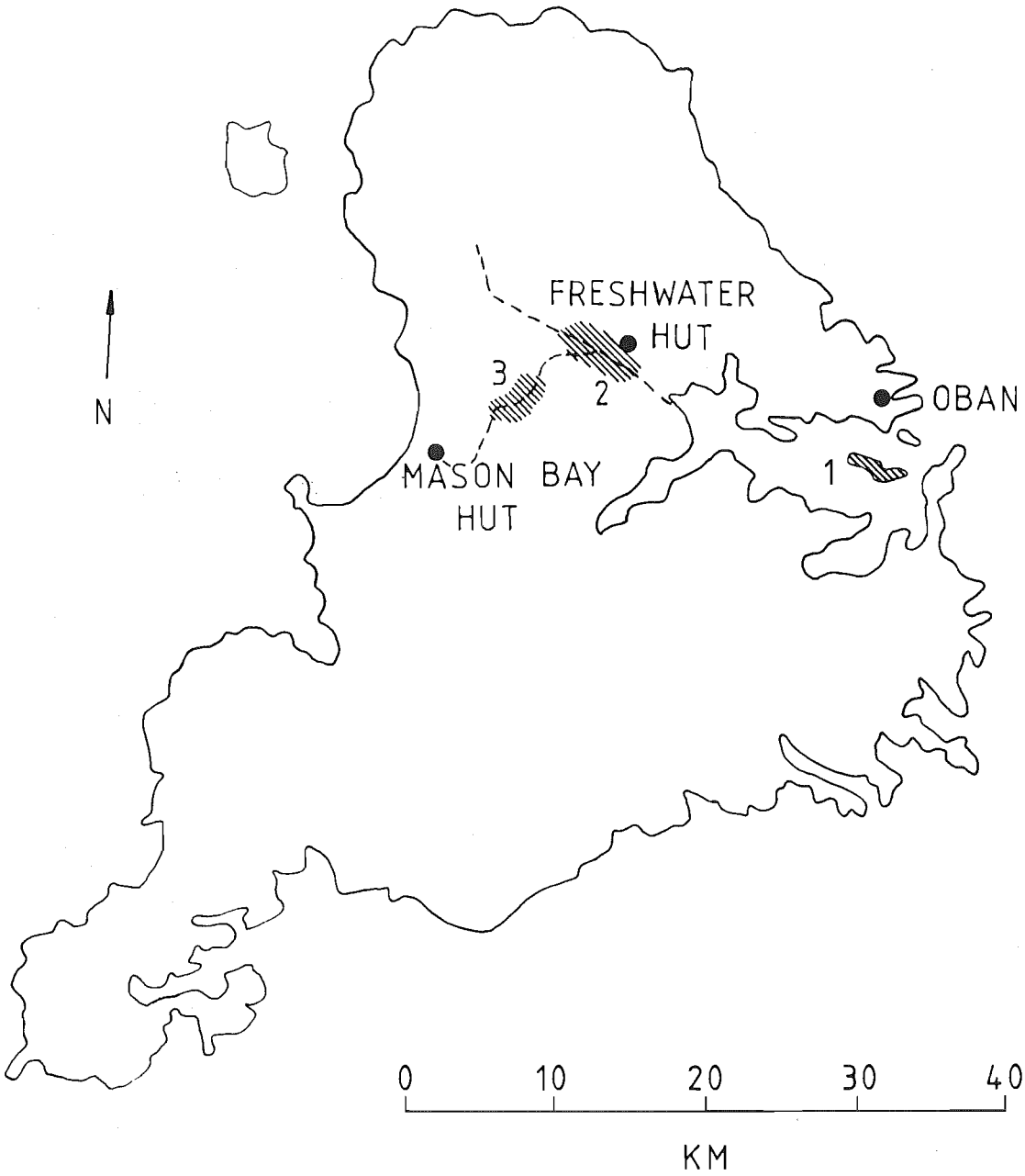

Fig. 2.3. Map of Stewart Island. Hatched areas show localities where brown creepers were recorded. 1. Ulva Island, 2. Freshwater Flat, 3. Mason Bay Track. Dotted lines indicate walking tracks (trails).

WEST BANK

This semi-native forest on the western bank of the Kowhai River is 0.5 km from Kowhai Bush. Its canopy is composed of kanuka, and Acacia spp. and is 5-10 m in height. An understorey is absent due to grazing by domestic sheep and cattle. The forest's boundaries are formed by the Kowhai River on the east and by farmland on the north, west, and south.

LAKE ROTORUA

Lake Rotorua is 8.5 km west of Kaikoura and 3.5 km southwest of Kowhai Bush. Surrounding the lake are discontinuous patches of forest. Both kanuka and manuka form the canopy which is 4-5 m high. The understorey here has also been eliminated by cattle and sheep.

MOUNT FYFFE

The native forest at the base of Mount Fyffe is contiguous with Kowhai Bush. It is bordered by farmland on the east and by the Kowhai River on the west. The canopy is 3-4 m in height and is composed of the same species as is found in Kowhai Bush. In a portion of the forest where grazing is allowed no understorey is present but where it is prevented introduced brooms and young kanuka and manuka form a dense low growth.

WAIMANGARARA RIVER

The Waimangarara River is 7.5 km north of Kaikoura and 5.5 km northeast of Kowhai Bush. The forest lies in the floodplain of the river and is composed of kanuka and manuka that forms a canopy 5-12 m high. The understorey is thick and dominated by Coprosma spp. and introduced brooms. The forest is surrounded by farmland but is tenuously connected

to native forest on Mount Fyffe.

STEWART ISLAND

Stewart Island lies 24 km off the southern coast of the South Island. Extensive stands of native forest cover much of the island.

Ulva Island, a State Forest Scenic Reserve, is a small island (260 ha) in Patterson Inlet, 4 km south of the town of Oban. White-tailed deer (Odocoileus virginianus) and feral cats (Felis catus) occur only occasionally on the island and ship rats (Rattus rattus), are numerous but controlled by trapping. A lowland podocarp-hardwood forest with a canopy height of 15-20 m covers the island. The dominant tree species are rimu (Dacrydium cupressinum), kamahi (Weinmannia racemosa), miro (Podocarpus ferrugineus),and Hall's totara (P. hallii). There is an extensive understorey composed of lancewood (Pseudopanax crassifolium), Coprosma spp., wheki tree fern (Dicksonia squarrosa), and broadleaf (Griselinia littoralis).

Freshwater Flat, located on the western edge of Patterson Inlet and 18 km from Oban, is a marshy grassland with scattered dense stands of 2-3 m high manuka. Brown creepers were found exclusively in these stands. An understorey was absent.

The Mason Bay Track runs southwest between Freshwater Flat and Mason Bay. Tape recordings were made at a location ca. 5 km from the Freshwater Landing Hut. There the vegetation is similar to that found in Freshwater Flat except that the trees are taller (3-5 m).

CHAPTER 3

METHODS

INTRODUCTION

The main study area for this investigation was in the southeastern end of Kowhai bush; selected for its low canopy (4-8 m) and open understorey. At the commencement of the work I banded ca. 80% of the brown creepers in this area. All observations dealing with the breeding ecology and social and communicatory behaviour of the species were made at this site.

The field work was begun in September 1979 and completed in December 1982. Daily trips were made to Kowhai Bush during each breeding season (September-January) and during the non-breeding season (February-August) trips of one week's duration were undertaken each month.

Birds were tape recorded in Kowhai Bush throughout the entire study period. In December 1979 and again in October 1980 birds were recorded in the West Bank forest, in January 1980 and November 1981 at Lake Rotorua and in October 1981 at the Mount Fyffe site. During October 1981 I tape recorded birds at Waimangarara River. Two field trips were made to Stewart Island; the first in February 1981 to Ulva Island and the second in August 1982 to Freshwater Flat and Mason Bay Track.

CAPTURE AND BANDING OF ADULTS

After attracting the brown creepers with recordings of songs or calls the birds were caught in mist nets which were 5.5 m long and 2.1 m high. Once netted, they were immediately weighed, measured and colour-

banded. Weights were obtained using a 30 ± 0.5 g capacity spring balance. The following linear measurements to the nearest 0.1 mm were taken with vernier calipers: bill length (dorsally from tip to junction of bill and skull), bill width (horizontally at base of exposed culmen), bill depth (vertically at base of exposed culmen), tarsometatarsus length (laterally from "ankle" joint [Articulatio intertarsalis] to articulation of folded toes) and wing length (minimum chord of unflattened and unstraightened wing from carpal flexture to tip of longest primary). Each bird then received a numbered New Zealand Wildlife Service aluminium band and a unique combination of coloured bands. In all 71 adults and 56 chicks were banded.

NESTS

A total of 52 brown creeper nests was studied. To reach most of these I used a 4.5 m aluminium ladder. Once the nest was located, the nest tree was marked with coloured plastic flagging. I measured with a graduated tape the following characteristics of the nest site: the height of the nest above the ground, the height of the nest tree, the height of the canopy, and distance between the rim of the nest and the vegetation just above the nest cup. Nests were removed, dried indoors for several weeks and weighed to the nearest 0.1 g. The following four nest measurements (±0.1 mm) were taken from those nests that had not held young: exterior and interior diameters of nests (measured at rim), exterior depth (measured from rim to base of nest) and interior depth (measured from centre of nest floor to rim surface).

EGGS

Eggs were weighed and measured within 6-12 h after being laid. Each egg was marked for individual identification with a number written

in soft pencil on the shell.

NESTLING GROWTH

The growth pattern of young brown creepers was studied by daily weighing nestlings and measuring their tarsi. Weights were obtained using either a 10±0.1 g or a 30±0.05 g capacity spring balance while tarsi were measured to the nearest 0.1 mm using vernier calipers. Weights and measurements of each nestling were taken at approximately the same time of day and if defecation occurred during weighing, the weight of the nestling and the fecal sac were added. Nestlings whose weight consistently declined were excluded from the analysis.

To determine if daily handling affected nestling growth rates, five nests that contained 15 nestlings were visited every three days and the resulting growth curve was compared to that obtained from nestlings visited every day. No difference could be found in the two growth curves (ANCOVA; $P > 0.05$) suggesting that daily handling had little effect on nestling growth rates.

PLOTTING TERRITORIES

A grid of reference points was set up in the main study area and used to determine the location of birds seen in the field. Reference points were 100 paces apart and were located along roads, fence lines and survey lines that crossed the main study area. The positions of these points were plotted onto a 1:4000 scale map of the main study area.

Locations of marked birds seen during the breeding season were determined by counting the number of paces from the sighting to the nearest reference point and the compass direction travelled to that point. If the sighted bird was vocally interacting with another conspecific this was noted. At the completion of each breeding season all

sightings for each bird were plotted onto a map of the study area. At least 15 sightings were obtained for each bird.

A bird's territory was defined as the area enclosing all sightings of that bird when it was interacting vocally with neighbours. The sizes of territories were calculated by tracing the outline of the territories onto graph paper and estimating the area from the relationship of 1 mm^2 on the map = 15.7 m^2 of territory.

MOVEMENT AND ORGANIZATION OF NON-BREEDING BIRDS

During the non-breeding season I investigated the movements and organization of adult and juvenile birds in the main study area. To accomplish this the following information was gathered:

1) Spacial location - The location of all marked birds was determined in the same manner as was described above for the breeding season. At the conclusion of each non-breeding season all sightings for each bird were plotted onto a map of the main study area.

2) Nearest association - When a coloured marked adult or juvenile bird was sighted in the field I noted the band combinations of any birds that were within 3 m of it. Each observation was noted only once regardless of the duration. These data were converted into a measurement of association between birds by using the coincidence index developed by Dice (1945):

Coincidence Index = $2h/(a+b)$

where h = number of samples containing both individuals,

a = number of samples having individual A, and

b = number of samples having individual B.

RECORDING PROCEDURE

A Uher 4000 Report L tape recorder and an AKG 900 microphone were

used to obtain all tape recordings. Hitachi UD7-90 magnetic tape was used at a tape speed of 19 cm/s.

In order to preserve all possible information about the context in which various vocalizations were performed and any accompanying behaviour, I kept field notes. These were either written down immediately or dictated onto the tape with the field recordings. The colour-band combinations of the birds were also noted on the recordings.

Male brown creepers rarely sang unless stimulated by the song of another male. Thus, to obtain some tape recordings, a loop tape of song was played with a hand held cassette tape recorder to stimulate singing. Recordings of the same individual obtained with stimulation and without were visually compared and the procedure appeared to have no obvious effect on the sequence or morphology of the notes making up the songs.

SOUND ANALYSIS

Recordings were analysed on a Kay Electric Company Model 6061 B sonagraph using the wide band setting and the "off" position on the automatic gain control. To keep sonagram quality consistent and to reduce measurement errors as much as possible, the VU meter on the sonagraph was maintained at -1 for the input level and -5 for the output level. With these settings I used a mark level of 1.5-2.5.

MEASUREMENT OF SONAGRAMS

Sonagrams of calls and songs were measured by placing a transparent sheet of millimetre graph paper over the sonagram and measuring (±1 mm) the appropriate parameters. For calls, I measured the length and frequency of call notes and the duration between notes. When measuring the sonagrams of songs I excluded from the analysis the interlude (see Fig. 6.1, p. 67) that occurs between consecutive songs

because it was not performed by all males. The following parameters were measured from song sonagrams: the total length of the song phrase, the length and frequency (taken at mid point of note) of notes making up the song and the duration of the intervals between notes. These metric measurements were converted to seconds and kilohertz using the relationship of 1 s = 102.6 mm and 1 kHz = 12.6 mm. The measurements obtained from sonagrams of songs were used to generate the following 16 song characters:

1) SL - total length of the song. (Taken from the first discernible mark to the last.)
2) NN - number of notes in song.
3) MLN - average length of notes making up the song. (The total length of all notes was divided by NN.)
4) VLN - standard deviation for the MLN.
5) MIBN - average length of intervals between notes. (The total duration of all intervals between notes was divided by the number of intervals between notes.)
6) VIBN - SD for the MIBN.
7) MXF - maximum frequency within the song. (Taken at the mid point of the note with the maximum frequency.)
8) MNF - minimum frequency within the song. (Taken at the mid point of the note with the minimum frequency.)
9) MFS - average frequency of entire song. (The sum of the frequencies of all notes was divided by the total number of notes.)
10) VFN - SD for the MFS.
11) MCNL - average change in length of adjacent notes. (The sum of the absolute value of the changes in the durations of notes was divided by the number of changes.)
12) VNLC - SD for the MCNL.

13) MCIBN - average change in duration of intervals between notes. (The sum of the absolute value of the changes in the duration of the intervals between notes divided by the number of changes.)

14) VCIBN - SD for the MCIBN.

15) MCF - average change in frequencies of adjacent notes. (The sum of the absolute change in the frequencies of notes was divided by the number of frequency changes.)

16) VFC - SD for MCF.

TRANSFER EXPERIMENT

On the 28 July 1981, I transferred 4 males from Lake Rotorua to Kowhai Bush. Before they were shifted, all males were weighed, measured, banded and individually coloured marked and their songs were recorded. The four birds were released together into Kowhai Bush ca. 0.5 km from the main study area.

During October of 1981 two of the males, MR-BB and MR-RB, were found. MR-RB had set up a territory near where I had originally released the birds and MR-BB within the main study area. Both males had acquired mates from the local population.

The songs of both males were re-recorded throughout the 1981-82 breeding season and their singing behaviour was monitored. MR-RB's song was recorded again at the beginning of the 1982-83 breeding season.

FIELD PLAYBACK EXPERIMENTS

Field playback experiments were utilized to investigate various aspects of brown creeper singing behaviour (see Chapt. 8, 9 and 10). In all experiments a Uher 4000 Report L tape recorder was used for playback with a consistent tape speed of 19 cm/s. The tape recorder was equipped

with a 15.2 cm external loudspeaker which was placed in a tree 1.5 m off the ground. I observed the birds while concealed behind vegetation 9 m from the position of the loudspeaker and used a digital stopwatch to time their responses. All the males I tested had established territories and their mates were incubating eggs. The experiments were conducted between 800-1100 NZST.

RESPONSES TO DIFFERENT DIALECTS

Playback experiments were conducted to determine the responses of territorial males from Kowhai Bush and Lake Rotorua to songs from different song dialects (see Chapt. 8). Songs used in these experiments came from Kowhai Bush, Lake Rotorua and West Bank (Fig. 3.1). Each male tested was exposed on successive days to three conditions presented in random order: a control period during which no song was played back but the playback equipment was in place, the playback of a local song and the playback of a song from one of the other two populations. Responses were observed for a period of 6 min during each condition; 3 min with the playback song on and 3 min with it off. The songs were played at a rate of 6 songs/min, the average delivery rate of a singing territorial male. Playback sound volume was constant and approximated that of a normal singing male. During all the experiments the loudspeaker was placed in the centre of the subject's territory.

A total of four experiments, two in Kowhai Bush and two at Lake Rotorua, was completed. In Experiment 1, 20 Kowhai Bush males were exposed to a control period, a local Kowhai Bush song and to a foreign Lake Rotorua song. During Experiment 2, 12 males at Lake Rotorua were observed during a control period, a local Lake Rotorua song and a foreign Kowhai Bush song. Thirteen Kowhai bush males were the subjects of Experiment 3 and were exposed to a control period, a local Kowhai Bush

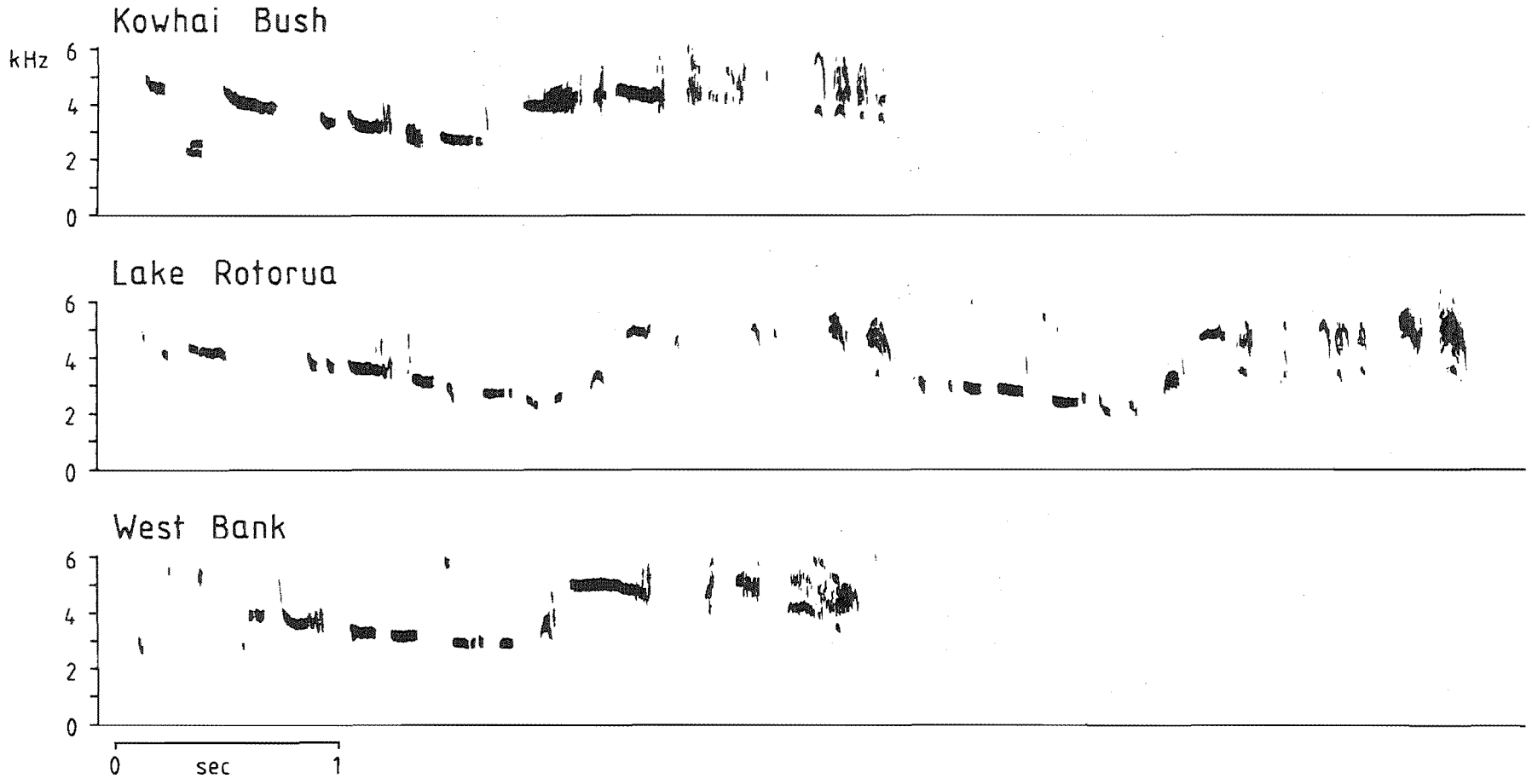

Fig. 3.1. Sonagrams of the three songs used in the playback experiments testing males' responsiveness to songs from different localities.

song and to a foreign West Bank song. In Experiment 4, 14 Lake Rotorua males were exposed to the control period, a local Lake Rotorua song and to a foreign West Bank song. Experiment 1 was conducted on the 8, 9, 11 and 12 of October 1980, Experiment 2 on the 13, 14, and 15 October 1980, Experiment 3 was conducted on the 9, 10, 12 and 13 of October 1981 and Experiment 4 on the 14, 15, 16 and 17 October 1981.

Categories of responses measured during the experiments consisted of the number of songs sung during the first 3 min of observations (during the playing of the playback tape), the number of songs sung during the second 3-min period (immediately after the playback tape was turned off), the latency of singing, the latency of approach to within 5 m of the loudspeaker, closest approach during the first 3-min period and the closest approach during the second 3-min period. Time was measured to the nearest second. Approach distances were ranked so that distances greater than 5 m from the loudspeaker had a rank of 0; distances between 2-5 m a rank of 1; distances between 1-2 m a rank of 2 and distances of 1 m or less a rank of 3.

NEIGHBOUR/STRANGER DISCRIMINATION AND ASSOCIATIVE LEARNING

Two types of experiments were conducted; the first compared male's responses to songs of neighbours and strangers, and the second investigated the role and nature of associative learning in neighbour/stranger recognition (see Chapt. 9).

Type 1 Experiments

Type 1 experiments were conducted on seven Kowhai Bush males whose territorial boundaries had been determined before the experiments. Each of the males was exposed on successive days to three conditions which were presented in random order; control (no song was played back but the playback equipment was set up), playback of a neighbour's song and

playback of a stranger's song. The responses of the males were noted over a period of 6 min for each condition; 3 min when the playback tape was on and 3 min when the tape was turned off and there was silence. Songs were played at a rate of 6 songs/min and the sound volume was adjusted to approximate that of a normally singing male. When a neighbour's song was played the loudspeaker was placed at or just inside the territorial boundary that was common with that neighbour. Playback of the stranger's song took place at the same location. The stranger's song used during the experiments was recorded from a male whose territory was 1.0 km from the main study area but in Kowhai Bush.

The categories of response measured during each experiment were the same as those used in testing responses to different dialects. The neighbour/stranger discrimination experiments were conducted on the 18, 19 and 20 October 1981.

Type 2 Experiments

Type 2 experiments were divided into two parts. The first was performed on the neighbours and the second on the non-neighbours of MR-RB, one of two males transferred into Kowhai Bush from Lake Rotorua who throughout the experimental period sang the Lake Rotorua theme. During the first part of the experiment, I exposed six Kowhai Bush males whose territories were 1.0 km from MR-RB's territory to three different songs, a local Kowhai Bush song, MR-RB's song and a song from another Lake Rotorua male on consecutive days, presented in random order. The local Kowhai Bush song was recorded from a male that was a non-neighbour of all of the males tested. For the second part of the experiment, I compared the responses of MR-RB's three neighbours to the same three playback songs. The songs were presented in random order on consecutive days and then played to the bird a second time during the next three consecutive days. Thus each of MR-RB's neighbours was tested twice.

All the experiments lasted 3 min during which three response categories were noted: the number of songs sung, the latency of singing and the closest approach distance to the loudspeaker. Latency of singing was measured to the nearest 1 s using a stopwatch and the closest distances were ranked as described above. The loudspeaker was placed 1-2 m inside the territorial boundary. The experiment was carried out on the 14-19 October 1982.

STRENGTH OF RESPONSE AND PERCENTAGE OF SONGS OVERLAPPED

These experiments were designed to see whether the percentage of playback songs that were temporally overlapped varied with the placement of the loudspeaker (see Chapt. 10). A total of ten males in the main study area whose territorial boundaries had been determined previously were tested. The loudspeaker was placed at three locations: the subject's territory centre, the boundary of the subject's territory and 5 m outside the subject's territory. The playback consisted of 18 repetitions of a song recorded 1.0 km from the main study area. Spacings between songs on the tape were not even.

The experiment was run for 3 min during which I noted the number of the playback songs that the subject temporally overlapped. This experiment was conducted on the 21 and 22 October 1981.

TESTING THE PLAYBACK EQUIPMENT FOR DISTORTION

After completing the playback experiments, I tested the experimental apparatus to see if any distortion of songs could have occurred. The recordings from Kowhai Bush and Lake Rotorua which had been used for the playback experiments were examined.

The tests were carried out on 15 May 1983 in a garden of native plants on the campus of the University of Canterbury, Christchurch. The

Table 3.1 Mean ± SD of minimum and maximum frequencies of ten songs recorded originally from a male and those same songs re-recorded after being played through a 15.2 cm loudspeaker. Songs analysed were from Kowhai Bush and Lake Rotorua.

	Original		Re-recorded	
	min.	max.	min.	max.
Kowhai Bush	4.38±0.033	7.57±0.026	4.39±0.026	7.58±0.033
Lake Rotorua	4.10±0.028	7.88±0.032	4.09±0.032	7.88±0.032

weather was dry with no wind or cloud cover. The tapes were played through the same system as was described above. The songs were re-recorded at a distance of 3 m using a second Uher 4000 Report L tape recorder, a Nakamichi CM-300 microphone and a tape speed of 19 cm/s.

Sonagrams of both the original recordings and the re-recorded songs were produced. To see if distortion had occurred, I measured the minimum and maximum frequencies within the songs and also visually inspected the sonagrams for any alteration in their harmonic structure. A Student's t-test was used to compare the frequencies of the original and the re-recorded songs.

No differences (t-test; $P>0.05$) were found between the original and the re-recorded playback songs (Table 3.1). This suggests that brown creeper songs were not distorted by the experimental equipment. In addition, the harmonic structure of the playback recorded songs was not altered.

TERMINOLOGY

The terminology used to describe the components of songs as observed on sonagrams, and the general vocal behaviour of the species follows that of Armstrong (1963), Mulligan (1966), Thorpe (1972), Lemon (1975), and Baptista and Johnson (1982). They are:

Song - a relatively complex pattern of sound that is

stereotyped.

Interlude - a stereotyped pattern of notes and/or trills which was used by some males between consecutive songs.

Call - a sound of brief duration and simple structure.

Note - a sound producing a continuous trace on the sound spectrograph.

Song type - one of the distinctive songs in the repertoire of an individual which is repeated in a stereotyped manner.

Theme - a song pattern in a population often shared by several, but not necessarily all members of the population.

Bout - a discrete unit of behaviour which is delimited by the temporary cessation of the behaviour.

Duetting - an antiphonal or polyphonal vocal display between a mated pair of birds.

Alternate singing - interactional singing between neighbouring territorial males in which there is little or no temporal overlapping of the two males songs.

Unison singing - a form of interactional singing in which a male rapidly responds and temporally overlaps the songs of another male.

Song dialects - a locally dominant theme or group of themes that have certain characters in common. The term implies similarity of theme or themes within a population and dissimilarity between populations.

Whistle - a note relatively free of frequency modulation.

Buzz - a frequency modulated whistle.

Slur - a whistle which either falls or rises in frequency.

Trill - a consecutive series of similar notes. The repetition within a trill could be either fast or slow.

CONVENTIONS

1) All means are given with ± the standard deviation of the mean.
2) The term "recorded" means that the vocalization was tape recorded.
3) Throughout the thesis individual birds are identified by their band combinations. I have used the following abbreviations: M = metal (aluminium), W = white, R = red, Y = yellow, B = blue, G = green. The colour-band combination(s) on a bird's right leg is listed first, followed by a hyphen and then the combination on the left leg. The first band listed is that which is highest on the bird's leg. Five males were unbanded but were recognisable by their song patterns and are identified by the letters UB-M (unbanded male) followed by a 1,2,3,4 or 5.

CHAPTER 4

THE BREEDING ECOLOGY OF THE BROWN CREEPER

INTRODUCTION

The breeding strategies of birds are diverse and have evidently differentiated in response to a variety of environmental variables including most prominently the predictability and stability of food supplies (Ricklefs 1968, O'Connor 1977a, Case 1978). Although there have been numerous studies dealing with avian breeding habits, few species inhabiting temperate oceanic islands have been investigated. Oceanic islands, such as New Zealand, typically have mild climates with little seasonal variation (Hurnard 1978), resembling in this respect most tropical continental regions.

Although the brown creeper is a locally common New Zealand forest bird, little is known of its breeding habits. Thus, a major objective of this study was to describe the basic breeding strategy of the brown creeper; information which was necessary for the interpretation of its social organization and communicatory behaviour.

Several New Zealand passerines are known to have protracted breeding seasons, produce large eggs relative to their body sizes, and have slow development rates (Gray 1969; Best 1973, 1975; Gill 1982; Powlesland 1983). In addition, annual adult mortality has been reported to be low in the grey warbler (Gerygone igata; Gill 1982) and the New Zealand robin (Petroica australis; Powlesland 1983). These are not typical breeding patterns for passerines inhabiting temperate continental regions but more closely resemble those from the tropics. Therefore a second objective of this study was to compare my findings with those of species from both New Zealand and the tropics and discuss those common

environmental factors that may have been responsible for shaping the breeding strategy of the brown creeper.

RESULTS

THE BREEDING SEASON

During the three breeding seasons spent in Kowhai Bush, I observed the seasonal patterns of laying, hatching and fledging in the brown creeper (Fig. 4.1). Because sample sizes for each season were small all data were pooled. When the exact date of an event was unknown an estimate was calculated by extrapolating from a known date using average values for the lengths of incubation and nestling periods. No serious errors are introduced by this technique since the data are grouped by weeks (Cramp 1955). One-third of the dates plotted in Fig. 4.1 were obtained by extrapolation.

In Kowhai Bush, eggs were laid in two peaks over a 18-week period, between the third quarter of September until the third quarter of January (Fig. 4.1 A). The earliest known second clutch which followed the fledging of an earlier brood was started on 17 November 1981. Subsequently, all clutches begun before 17 November and their associated nests and nestlings were defined as "early" and those started after as "late".

Seventeen weeks had elapsed from the time the first eggs hatched in the second quarter of October until the last eggs hatched in the first quarter of February (Figure 4.1 B). Fledging of nestlings occurred over an equal period from late October until the third quarter of February. Starting from the first observation of nest building on 10 September 1980, the total length of the breeding season of brown creepers in Kowhai Bush was 24 weeks or ca. 5.5 months.

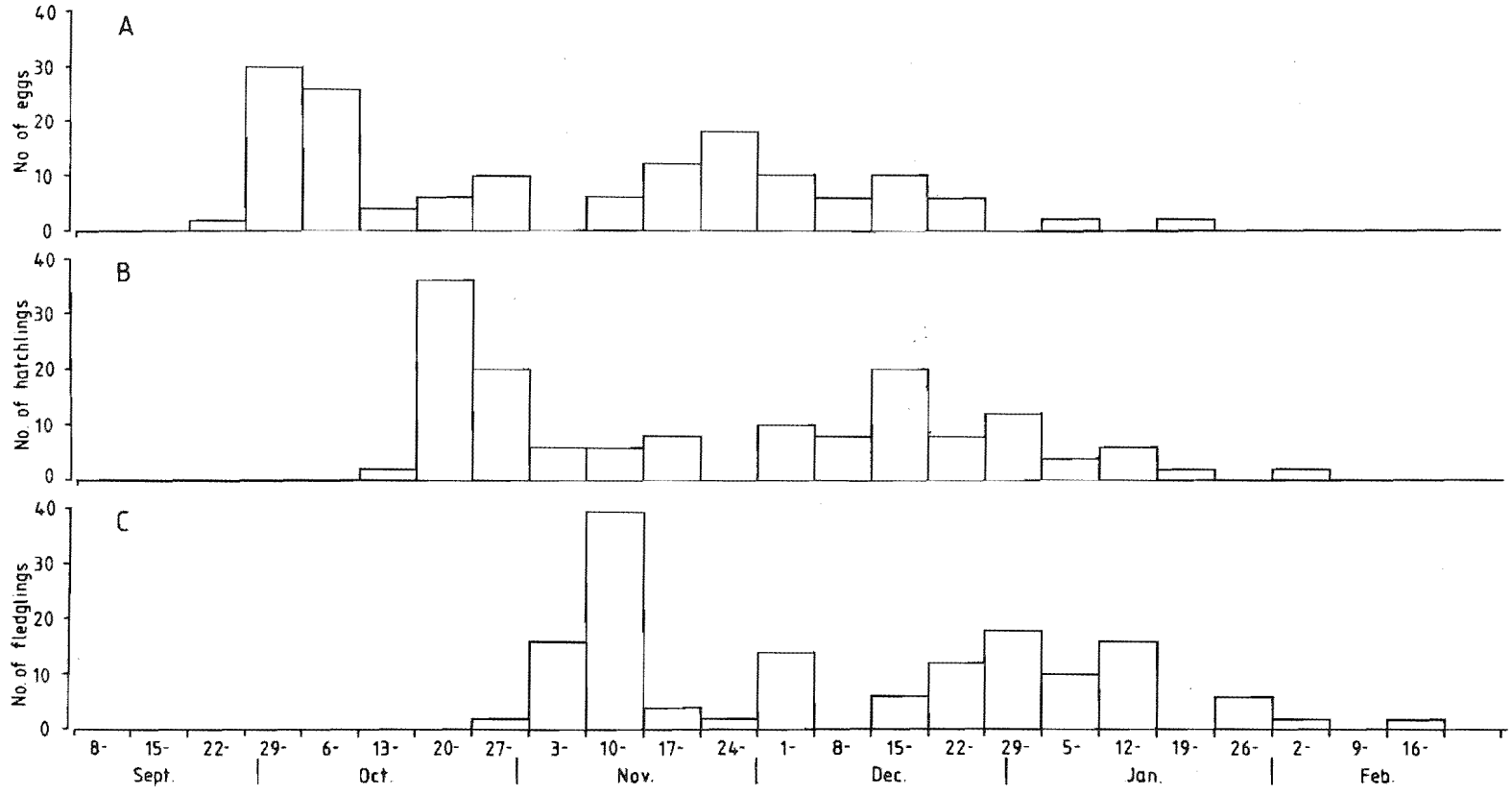

Fig. 4.1. Patterns of three events in the breeding of brown creepers at Kowhai Bush. Weekly frequencies are shown of A. laying, B. hatching, C. fledging.

COURTSHIP AND COPULATORY BEHAVIOUR

Courtship Feeding

Courtship feeding was seen on 21 occasions, during both the egg laying and incubation periods of early nests but not during late breeding attempts. This behaviour was always performed away from the nest although feeding on the nest has been reported by Soper (1972). The female fed by approaching the male, fluttering her wings and giving zheep calls (description of calls and displays: Chapt. 6).

Precopulatory and Copulatory Behaviour

Males frequently chased their mates just before copulation. Chasing which lasted 2-5 min, consisted either of long rapid flights by the two birds through the forest canopy or quick hops and short flights through dense vegetation. Both sexes gave chatter calls and males performed wing flutter during chases.

Females signalled their readiness for copulation by assuming the crouching posture and allowing the male to approach. The female then displaced her tail slightly to one side and the male mounted. Mounting normally lasted less than 10 s but was often repeated several times. While mounted the male continued to flutter his wings and to give the chatter call. In contrast, the female remained still and silent during copulation. All observed copulations occurred in dense vegetation.

If females were not receptive to their mates' advances they spread their tails and continued to hop from perch to perch. In this case chasing continued until either copulation finally took place or the male was distracted by the singing or calling of a male near by.

Mate Guarding

During the early stages of the breeding cycle males spent much of their time close to their mates. While females foraged or

collected nesting material, their partners usually hopped about from perch to perch, 2-3 m away. When behaving in this manner males seldom fed but assumed a searching posture. Mate guarding commenced a few days before nest building began and continued until the second or third egg was laid. This behaviour was observed during all nesting attempts but only intermittently during late nestings if the male was feeding fledglings.

NEST AND NEST SITE SELECTION

The nest of the brown creeper consisted of a tightly woven cup, the outer layers of which were composed of strips of kanuka bark and dried moss held together with spider silk. The inner surface of the cup was lined with fine dried grasses and a few feathers or sheep's wool. The feathers were rarely those from brown creepers.

The average nest weight was 11.4 ± 1.94 g (n=52). The nests were elliptical in outline from above, had a maximum outside diameter of 9.2 ± 0.47 cm (n=52) and a maximum inside diameter of 4.8 ± 0.40 cm (n=38). The inside depth of the cup was 4.2 ± 0.76 cm (n=38) while the outside depth of the nest was 7.4 ± 1.16 cm (n=52).

Nest Building

As believed by Falla et al. (1979), only females collected nesting material and built the nest. Most building took place in the early morning before 1000 h NZST and occurred in 10-15 min bouts interspersed with spells of feeding.

It was difficult to determine when a female began and completed her nest so the time required for nest building was only roughly approximated. Six early nests were completed in 7-17 days ($\bar{x}$= 11 days) and the two nests which were built after previous nesting attempts required 5 and 6 days for completion.

Table 4.1 Six characteristics of brown creeper nest sites.

	N	Mean	SD	Range
Nest height (m)	52	4.7	1.52	1.6 - 9.4
Tree height (m)	52	5.3	1.65	1.8 - 11.3
% tree height	52	88.2	8.34	60.0 - 98.4
Canopy height (m)	52	5.8	1.48	3.2 - 11.3
% canopy height	52	82.4	17.38	35.6 - 98.4
Foliage roof above nest (cm)	52	7.7	3.08	3.8 - 15.2

With 10 early nests there was a delay of 2-6 days ($\bar{x}$=3.1 days, n=10) between completion and the laying of the first egg. The delay was 2 and 3 days for the two late nests.

Nest Placement

Of 52 nests examined, 48 were built in kanuka, 2 in Coprosma spp. and 1 each in a Monterey pine (Pinus radiata) and a bush lawyer (Rubus squarrosus). Nests were placed in the upright forks formed by 3-4 small branches; the nests being tightly attached to these branches by spider silk and fine grasses.

Nest Site Characteristics

The data characterizing all nest sites were pooled because no yearly differences or differences between early and late nests were detected for any of the characters (t-test; P>0.05; Table 4.1). Brown creepers generally built their nests high in the forest (88.2% of the total nest tree height and 82.4% of the total canopy height). Furthermore, the nest was normally positioned under a roof of dense vegetation which was 7.7 ± 3.08 cm above the rim of the nest.

EGGS

Colour

The ground colour of brown creeper eggs, as noted by Falla et al. (1979) and Oliver (1955) was highly variable. In this study, three

distinctive egg colours were discerned: white, light pink, and dark pink. Similar colour types were found in Kowhai Bush by Gill et al. (1980). Thirteen eggs held by the Canterbury Museum, Christchurch could be divided into the same three colour types plus an additional one; light brown. Of 57 Kowhai Bush eggs examined, 25 were white and 26 were light pink. The remaining 6 eggs were dark pink and these were all laid by one female who consistently produced eggs of this colour. The colour of eggs was consistent within clutches and between clutches from the same female.

The pattern of reddish brown, dark brown or purple markings on eggs varied considerably between females from almost non-existent to intense. These markings of well defined spots, streaks or diffused blotches, were always concentrated at the blunt end of the egg. The patterns varied little within clutches or between clutches from the same female.

Dimensions

Brown creeper eggs were 18.4 ± 0.68 mm long x 14.2 ± 0.32 mm wide (n=36). The lengths of eggs varied with clutch size with eggs from 2-egg clutches 19.3 ± 0.42 mm (n=4), from 3-egg clutches 18.7 ± 0.69 mm (n=16) and from 4-egg clutches 17.9 ± 0.37 mm (n=16). Eggs from 3-egg clutches were significantly longer than those from 4-egg clutches ($t=4.00$; $P<0.001$). The sample size for 2-egg clutches was too small for comparison with the others.

In contrast, egg width remained constant regardless of clutch size. The average width of eggs from 2-egg clutches was 14.3 ± 0.27 mm wide (n=4) while those from 3 and 4-egg clutches were 14.3 ± 0.26 mm (n=16) and 14.0 ± 0.30 mm (n=16), respectively.

Weight

The average weight of eggs obtained within 6-12 h of laying was 2.0 ± 0.17 g (n=31) which represents 18.2% of the mean weight of an

adult female (11.0 g) (Cunningham 1984). Passerines that weigh 11.0 g, normally lay eggs which are ca. 12.5% of their total weight (Lack 1968: 184). Thus, female brown creepers produce eggs which are heavier than is typical for a bird of their size. Given an average weight for a brown creeper egg as 2.0 g, a female would need to weigh 15.0 g in order for the egg to represent 13% of her weight. The heaviest female caught during this study weighed 13.0 g 1-2 days before she began laying her 3-egg clutch and hence probably had partially formed eggs within her.

Egg weight varied with clutch size. Eggs from 2-egg clutches weighed 2.2 ± 0.10 g (n=4), 2.1 ± 0.12 g (n=11) from 3-egg clutches and 1.8 ± 0.11 g (n=16) from 4-egg clutches. The sample size for 2-egg clutches was, again, too small for valid comparisons to be made but the eggs from 3-egg clutches were on average heavier than eggs from 4-egg clutches ($t=7.50$; $P<0.001$).

Clutch Size

Of 42 clutches, 42.8% contained 4 eggs, 42.8% contained 3 eggs and 14.3% contained 2 eggs. The average clutch size for all nests was 3.3 ± 0.72 eggs (n=42). Early and late clutches differed in size ($t=5.29$; $P<0.001$): for early nests they were 3.7 ± 0.47 eggs (n=22) and for late nests 2.8 ± 0.63 eggs (n=20). This difference resulted because early nests contained more 4-egg clutches and fewer 3-egg clutches than late nests. No 2-egg clutches were found in the early nests but 30.0% of the late nests contained 2 eggs.

INCUBATION

Incubation Behaviour

Only females developed brood patches and incubated the eggs. At all early nests and most late ones, incubation began the day the last egg

was laid. However, the females began incubation in two late nests before the last egg was laid. In another two late nests, hatching was asynchronous suggesting that incubation may have begun before clutch completion.

By direct observation I determined that females spent an average of 70% (n=29 bouts of 3 h observations; range= 53-85%) of the daylight hours on the nest. Nest attentiveness usually declined during the incubation period but this trend was not always obvious as weather conditions also affected it; attentiveness being greater on cold or rainy days.

Length

The average length of the incubation period (interval between laying of last egg and hatching of that egg) for 38 clutches was 19.2 ± 1.10 days.

NESTLING PERIOD

Length

The time between the day of hatching (day 0) and the day of fledging defined the length of the nestling period which was 20.0 ± 0.60 days (n=41). This value, however, may be conservative since some of the nestlings probably fledged earlier than expected. I found that 15-20 day old nestlings had a tendency to leave the nest prematurely if disturbed by the observer.

Weight Changes in Nestlings

Weight of nestlings increased rapidly from day one to day 11, after which it slowed until a peak weight of 12.2 g was reached on day 14 (Table 4.2). From day 14 to fledging, the average nestling weight declined slightly to 11.7 g; a weight loss of 4.1%.

Table 4.2 Weights (g) and tarsal lengths (mm) of nestling brown creepers.

Age	Weight				Tarsus			
(days)	N	Mean	SD	Range	N	Mean	SD	Range
0	31	1.5	0.10	1.3 - 1.6	31	7.6	0.47	6.8 - 8.4
1	30	1.8	0.13	1.6 - 2.0	30	8.5	0.30	8.1 - 8.8
2	31	2.6	0.28	2.2 - 3.0	31	9.3	0.50	8.5 - 10.2
3	32	3.3	0.25	3.0 - 3.6	32	10.7	0.54	10.0 - 11.3
4	30	4.2	0.39	3.2 - 4.6	30	12.5	1.16	10.8 - 14.7
5	30	5.2	0.45	3.8 - 5.8	30	13.4	1.08	11.1 - 14.7
6	32	6.3	0.59	4.9 - 7.1	32	15.1	1.42	12.4 - 16.6
7	29	7.4	0.74	5.4 - 8.5	29	16.6	1.29	13.5 - 17.9
8	31	8.7	0.92	6.5 - 10.5	31	18.2	1.68	15.4 - 20.0
9	32	9.7	0.73	8.0 - 10.5	32	20.2	1.63	16.7 - 21.8
10	30	10.3	1.09	8.2 - 11.7	30	21.2	1.54	17.4 - 22.7
11	30	10.9	1.12	8.6 - 13.0	30	22.6	1.14	20.8 - 24.0
12	30	11.2	1.20	9.0 - 13.0	30	23.3	1.44	20.8 - 24.7
13	30	11.9	1.32	9.7 - 13.2	30	24.2	1.10	21.5 - 25.9
14	31	12.3	1.44	10.5 - 14.5	31	25.4	1.13	23.0 - 26.7
15	32	12.2	0.94	11.0 - 14.0	32	25.5	1.09	25.1 - 26.1
16	19	12.5	1.21	11.2 - 14.0	19	26.0	1.00	25.1 - 27.2
17	14	12.2	1.20	11.0 - 14.0	14	26.0	1.03	25.1 - 27.3
18	12	12.0	1.00	11.0 - 14.0	12	26.4	1.11	25.2 - 27.7
19	12	11.7	1.10	10.3 - 13.9	12	26.4	0.95	25.2 - 27.7
20	12	11.7	0.96	10.2 - 13.8	12	26.4	0.90	25.4 - 27.7

For comparative purposes I used Ricklefs' (1967) graphical technique for fitting equations to growth curves. The model which best described the growth curve of brown creeper nestlings was a logistic equation using a maximum weight or asymptotic weight of 12.5 g (Fig. 4.2). Once the proper equation and asymptotic value were determined several parameters which allowed interspecific comparisons of growth curves to be made were calculated (Ricklefs 1967, 1968). The rate constant, K = 0.353, indicates a slow growth rate and the ratio of the asymptote of the growth curve to the adult body weight, R = 1.02.

To investigate the effect of brood size on nestling growth rates, I compared regression coefficients of growth curves for broods of two, three and four. Although there was a tendency for nestlings from larger broods to weigh less than those from smaller broods, the growth rates were not significantly different (ANCOVA; $P>0.05$).

Tarsal Growth in Nestlings

A newly hatched nestling had an average tarsal length of 7.6 mm while at fledging it was 26.4 mm (Table 4.2). No differences were found in the tarsus growth curves for broods of two, three and four (ANCOVA; $P>0.05$) suggesting that tarsus growth is also independent of brood size.

Maturity of Birds at Fledging

At the time of fledging young brown creepers had nearly attained adult size in all measured characters except wing length (Table 4.3). For example, the average tarsus length of fledglings was 98.9% of the average adult tarsus length while the average wing length of fledglings was only 79.8% of the adult wing length. Observations I made of the locomotory activity of recently fledged brown creepers revealed that the muscular development of their legs was much greater than that in their wings. Fledglings were capable of running extremely well on the ground but were unable to sustain flight over distances greater than 2-3 m.

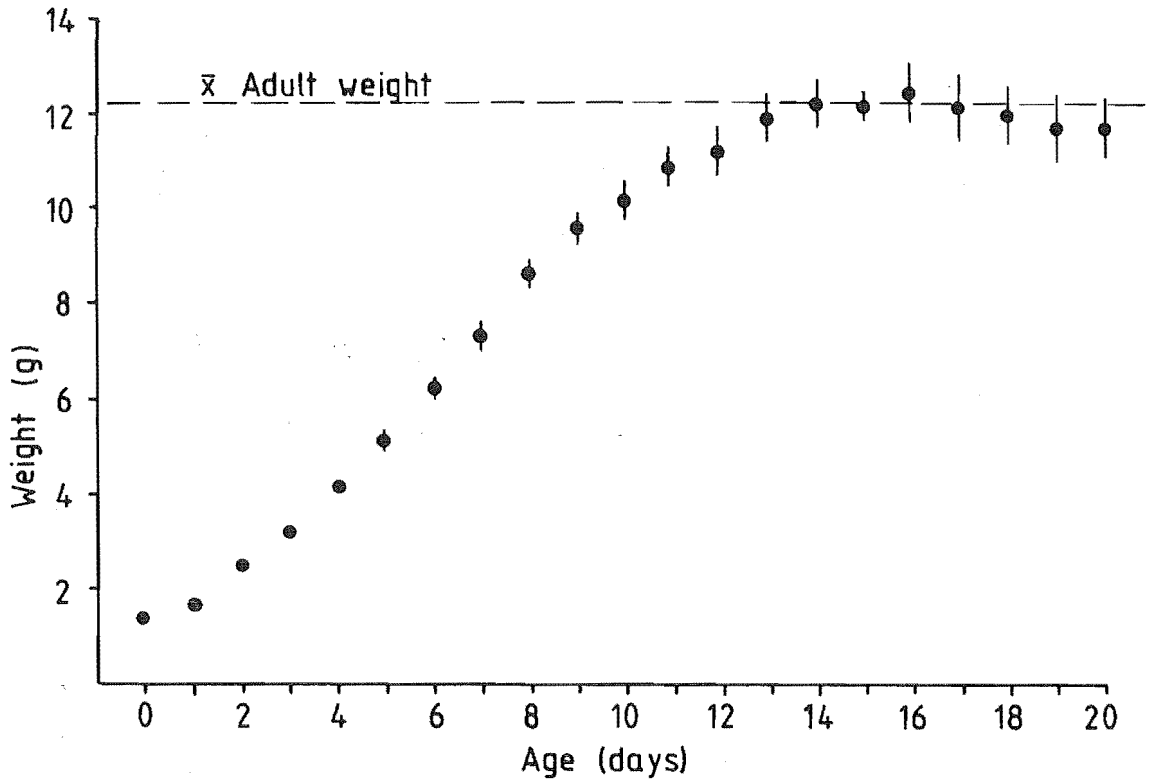

Fig. 4.2. Weight growth curve of nestling brown creepers. Vertical lines represent ± 2 SE (see Table 4.2 for precise weights and sample sizes).

Table 4.3 Body measurements of ten brown creeper fledglings.

	Mean	SD	% of adult measurement
Weight (g)	11.7	0.83	96.1
Bill length (mm)	12.1	0.93	96.0
Bill width (mm)	3.4	0.18	97.1
Bill depth (mm)	3.3	0.32	89.2
Tarsus length (mm)	26.4	0.60	98.9
Wing length (mm)	46.9	1.59	79.8

FLEDGLING PERIOD

Fledglings spent 35-65 days with their parents before becoming independent and were fed by both parents unless the female had begun to renest. During the first week, the young huddled together regardless of weather conditions during the daylight hours and the adults took food to them. As their wings became stronger and tail feathers grew, the young began to follow the foraging parents, begging loudly and fluttering their wings whenever food was caught. Eighteen to twenty days after fledging, when the young were capable of catching their own food, they continued to beg and wing flutter. The survival of dependent fledglings was high. Of 38 banded nestlings that fledged, at least 87% survived for more than 20 days.

Once independent, fledglings remained in stable sibling groups which dispersed varying distances from their natal territories until just before the next breeding season (p. 59, Chapt. 5). Of seven sibling groups I watched, one remained partially within its natal territory throughout the winter. Another five were found ca. 350, 480, 1050 and 1236m from their parental territories. The last flock could not be found after it left the main study area.

TERRITORIALITY

Brown creepers were monogamous and nested solitarily within their territories in which all nesting, courtship and mating activities took place and from which most food was obtained.(Hinde [1956], following Mayr [1935] calls this a type "A" territory). Pairs remained on these territories throughout the year, defending them against other pairs (see Chapt. 5). During the non-breeding season and early in the breeding season both sexes sang and defended territorial boundaries. Once egg laying commenced, however, territorial defense was performed primarily by males. After territorial borders had been defined trespassing into neighbouring territories was rare (Chapt. 10, p. 174).

Physical fighting between birds was seen only three times; either early in the breeding season or when the activity centres of pairs changed bringing the pairs into contact with different neighbours. Fighting normally began in the branches but once the combatants were holding each other with their feet and pecking with their bills they fell with wings fluttering releasing their hold on each other just before reaching the ground. Once on or near the ground the birds resumed attacking one another. Throughout the fight both birds gave chatter calls and occasionally one or both sang. Both males and females fought but only with its own sex.

The territorial boundaries of pairs remained consistent from year to year with only minor changes in boundaries (Fig. 4.3). The sizes of territories did not differ between years (t-test; $P>0.05$) and so all data were pooled. Brown creeper territories in the main study area had a mean size of 0.97 ± 0.21 ha ($n=39$).

PAIR-BONDS

Brown creeper pair-bonds were maintained year round (Chapt. 5).

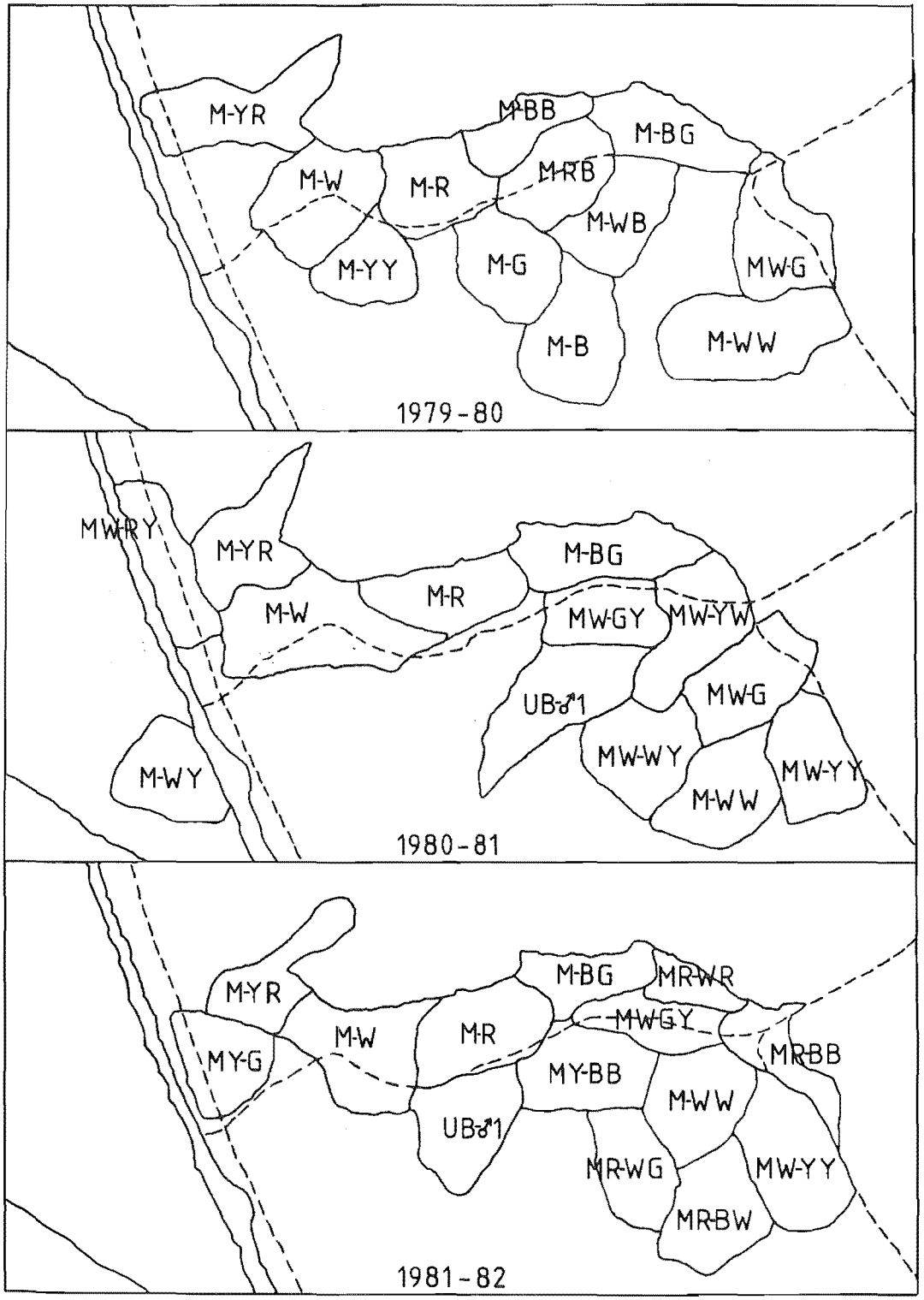

Fig. 4.3. Maps of the main study area (Kowhai Bush) showing the spacial arrangement of territories during the breeding seasons of 1979-80, 1980-81, and 1981-82. Letters indicate the band combinations of male territory owners. Dotted lines show the position of roads.

Table 4.4 Reproductive success of brown creepers in Kowhai Bush.

	Eggs laid	Young hatched	Young fledged	% Success		
				Hatching	Breeding	Nestling
Early (n = 21)	70	49	35	70.0	50.0	71.4
Late (n = 28)	84	49	21	58.3	25.0	42.8
Total (n = 49)	154	98	56	63.6	36.4	57.1

Also, they persisted over multiple seasons. Of 17 mated pairs in which both members were colour marked, 29.4% remained together for three breeding seasons, 35.3% for two, and the remaining 35.3% for only one. Therefore, of the original 17 pairs, 64.7 were paired for at least two breeding seasons. Swapping of mates was never observed and all changes in partners were due to the disappearance of one member of a pair.

REPRODUCTIVE SUCCESS, FECUNDITY, AND RECRUITMENT

Reproductive Success

Data for hatching success (proportion of eggs that hatched), breeding success (proportion of eggs laid that eventually yielded fledglings) and nestling success (proportion of nestlings that fledged) (Table 4.4) revealed that of the 154 brown creeper eggs laid, 64% hatched and 36% produced fledglings. Of the 98 nestlings produced, 57% fledged. Seventy percent of the eggs hatched in the early nests and only 58% in late nests; however, the difference was not significant (t-test; $P > 0.05$). Breeding success was 50% in early nests and only 25% in late nests. Similarly, in early nests 71% of the young fledged while 43% did so in late nests. Both the breeding success and the fledging success of early nests were significantly different from those of late nests ($t=3.25$; $P<0.01$ and $t=2.83$; $P<0.01$, respectively). These results suggest that fewer young are produced from late nests.

Most losses to both eggs and nestlings were due to predation, probably by stoats (Mustela erminea) or ship rats. A nest was classified as having been preyed upon if all contents were gone and there was no evidence that the eggs or nestlings had fallen out. Sixty-two percent of all egg losses and 66% of nestling losses were due to predators.

Moors (1975) has suggested that it is possible to distinguish between mustelid and rodent predation based on the condition and content of the remaining nest. Rodents tear the nest apart and often leave behind partly eaten material while mustelids leave an empty but structurally intact nest. Of 32 nests that were preyed upon, mustelids were probably responsible for destroying 90.6% and rodents 6.3%. The disappearance of nestlings from one nest which was found 1 m above its original position could not be attributed to either rodents or mustelids. Mammalian predation was unlikely because the nest tree had been isolated from neighbouring trees and had a 1 m wide aluminium skirt around its trunk to discourage mammals from climbing. I suggest that an Australasian harrier (Circus approximans), a species frequently seen flying low over the canopy, preyed upon this nest. When being removed, the nestlings, who were close to fledging, may have gripped the nest with their feet and dragged it up with them.

Fecundity

Twelve pairs of brown creepers were monitored to determine their fecundity (the total number of clutches laid by these pairs during one breeding season). These birds produced a total of 32 clutches making an average fecundity of 2.7 nesting attempts/pair per year. In monogamous species where both sexes feed the young the annual productivity of fledglings/breeding individual ,P , is equal to the nesting attempts/pair x clutch size x breeding success/2 (Ricklefs 1973). For the brown

creeper P=(2.7)(3.3)(0.364)/2=1.62 fledglings/adult per year.

Recruitment

The annual recruitment of juveniles into the breeding population was low. After spending ca. 40 h searching throughout Kowhai Bush, only four (10.5%) of the 38 fledglings banded were later found breeding. If the population I was studying was stable an alternative method for calculating recruitment is obtained by adult mortality (P)/fecundity (Ricklefs 1973). Recruitment in the main study area was 0.176/ 1.62= 0.11 or 11%. Thus the two approaches yield similar values and point to high juvenile mortality.

SURVIVAL OF ADULTS

The annual survival of adults was high. Of the 15 banded adults that nested in the main study area during the 1979-80 breeding season, at least 80.0% bred there the following summer. Similarly, of the 17 adults that bred during the 1980-81 season, 82.4% were found breeding in the 1981-82 season. Of the 20 adults which bred in 1981-82, 85.0% were found breeding at the beginning of the 1982-83 breeding season. The average annual survival of adults over these three years was at least 82.4%, leaving the annual mortality of adults at less than 17.6%.

The survival rate of adults over several years was also unusually high. Of 15 adults that nested in 1979, 10 (66.7%) were alive and breeding two years later. Seven (46.7%) of those original 15 adults were alive at the beginning of the fourth summer and were therefore at least 4 years old.

Life expectancy was high once birds became adults. Four males which had been banded in August 1979 and another one which had been banded in October 1979 were still alive in October 1984. Assuming that

these males fledged in January 1979, each was at least 5.8 years old when resighted the last time.

AGE AT FIRST BREEDING

Of the four birds banded as nestlings that were later found breeding, two were males and two females. Both males and one female bred in their first year after fledging while the second female was not found breeding until her second year. These data, though limited, suggest that brown creepers are capable of breeding their first year.

DISCUSSION

PROTRACTED BREEDING SEASON

The brown creeper has a long breeding season (September - February). Protracted breeding appears also to be a common phenomenon among other native New Zealand passerines. The New Zealand robin breeds from July to February (Flack 1973), the rifleman (Acanthisitta chloris) from August to January (G. Sherley pers. comm.), the fantail (Rhipidura fuliginosa) from August to February (Powlesland 1982), the grey warbler from July to January (Gill 1982), and the silvereye (Zosterops lateralis) from September to January (Fleming 1943).

The long breeding season of the brown creeper is probably related to the extended period during which conditions are suitable for reproductive activities (for a similar argument in relation to the grey warbler, see Gill 1982). The climatic regime of coastal New Zealand lacks marked seasonal fluctuations in temperature and a definite dry season (Hurnard 1978). These conditions allow insects to remain active throughout much of the year (Hurnard 1978) and stimulate plants to grow for protracted periods (Wardle 1978).

COURTSHIP FEEDING

Courtship feeding, as found in the brown creeper, is a common behaviour in passerines. Two hypotheses, which are not mutually exclusive, have been put forward to explain its occurrence. The first proposes that feeding helps in the development and maintenance of pair-bonds (Lack 1940, Andrew 1961, Armstrong 1965). My results, are not relevant to evaluating this hypothesis. Royama (1966) hypothesized that courtship feeding can assist females in obtaining extra food during the early stages of reproduction when their energy demands are high and he predicted that courtship feeding should occur primarily during egg laying. Male brown creepers were observed feeding their mates at this time, thus supporting the hypothesis. Feeding was also seen during incubation when females had little time to feed themselves but needed to replenish reserves depleted by egg production. This behaviour may, thus, be beneficial in supplying extra food to female brown creepers, thereby reducing the energy drain during reproduction and allowing the female to devote time to incubation. Feeding would also increase a male's fitness by allowing him to supply extra nutrients to the female who is producing the eggs he has fertilized.

MATE GUARDING

In monogamous species where males assist in rearing the young, males should be under strong selective pressure to ensure their genetic paternity and guard their mates from sexual advances of other males (Trivers 1972). It seems probable that the close following of females by their male partners, "mate guarding", has evolved as an adaptation to prevent cuckoldry, as argued by Power and Doner (1980) and Birkhead (1982).

Male brown creepers spent much of their time following their mates. Birkhead (1979) suggested that male guarding should be limited to the period when females are most fertile. Based on data for the duration of the female's fertile period, length of sperm storage and the competitive ability of sperm of varying age in the domestic chicken, Birkhead (1982) predicted that that guarding and copulation should start at least 3 days before the first egg is laid and cease ca. 3 days prior to the last egg to insure maximum protection against cuckoldry. Guarding in the brown creeper began before nest building and ceased when the second or third egg was laid. Thus Birkhead's prediction for the timing of the termination of guarding was met but not the timing of commencement. Perhaps, as Lumpkin (1981) has suggested, females manipulate their mates to begin guarding earlier. The early commencement of guarding would be advantageous for females because a guarding male could warn his mate of predators, and/or, chase off other courting males, preventing the female from wasting energy.

Birkhead (1981) also suggested that males might be disadvantaged by over-guarding their mates. This would occur when a male's guarding interfered with other important activities such as feeding fledglings. This helps to explain my observation that males guarded their mates less during second nesting attempts because there were often fledglings from the previous nest to be fed.

NEST SITE SELECTION

Brown creeper nests were well concealed with a dense roof of vegetation just above the nest cup. Predation is often cited as the selective force responsible for the construction of hidden nests. Before the introduction of mammals into New Zealand, the Australasian harrier and the New Zealand falcon (Falco novaeseelandiae) were probably the

principal predators of passerine nests (Fox 1977) and the thick covering of vegetation over the nest might have been an adaptation to deter them. Although nest predation by harriers or falcons was never directly observed, harriers were often seen flying low over the canopy and Redhead (1969) found that they rely heavily on the eggs and nestlings of passerines in the spring and summer. The roof of vegetation above the nest must also help protect the eggs and nestlings from rain and direct sun.

EGG SIZE

Brown creeper eggs are large, each constituting 18.2% of the female's weight. Other small New Zealand birds also lay large eggs. For example, Gill (1982) found that female grey warblers laid eggs that weighed 1.6 g or 23.3% of the mean adult weight of 6.4 g. Similarly, female riflemen weigh 7.0 g and lay eggs that weigh ca. 1.3 g or 18.6% of the female's weight (G. Sherley, pers. comm.).

Grant (1983) has shown that small Darwin's finches on the Galapagos islands lay disproportionately larger eggs than do larger bodied species. He suggests that the most important ecological factor influencing relative egg size in these birds is the rapid increase in food resources that occurs following the first heavy rain after the dry season. Grant argues that for body-size related energetic reasons the small-bodied finches should be able to take greater and faster advantage of the resource flush than the large bodied finches.

This argument, however, does not appear to apply in the New Zealand situation. As suggested earlier, in coastal New Zealand there is little seasonal variation in food abundance and food should be readily available for long periods of time. Secondly, in contrast to the

Galapagos, both large and small bodied New Zealand passerines appear to produce large eggs (Cunningham in prep.)

The low recruitment rate of young birds into the breeding population (see page42) indicates that juvenile mortality must be high. I suggest that brown creepers lay large eggs to compensate for this high mortality. By producing big eggs females produce large nestlings which develop into more mature fledglings which have a greater probability of surviving to breed. Skogland et al. (1952), Parson (1970), and Schifferli (1973) have shown that larger eggs produce larger nestlings which have a higher rate of survival.

CLUTCH SIZE

Ricklefs (1980) reports that the most common clutch size in tropical open-nesting species is 2-3 eggs while in the temperate and Arctic regions it is 4-6 eggs. The brown creeper's clutch size of 3.3 eggs is small for an open-cup nesting species. Other New Zealand species with the same type of nest construction also produce small clutches. The fernbird (Bowdleria punctata) has an average clutch size of 2.4 eggs (Best 1973), the fantail, 3.4 eggs (Powlesland 1982), and the robin, 2.7 eggs (Powlesland 1983). Clearly, open-cup nesting species in New Zealand produce small clutches that are more similar in size to tropical than to temperate or Arctic species.

The question of what factors may influence variation in clutch size in birds was first addressed by Lack (1947, 1954) who suggested that clutch size was adapted to correspond to the maximum number of young the parents could adequately nourish. Lack's original hypothesis was modified by Ashmole (1963) who argued that clutch size varies in direct proportion to the degree of seasonal fluctuations in the level of food resources utilized by a population. Ashmole, whose hypothesis has

recently been tested and supported by Ricklefs (1980) and Crowell and Rothstein (1981), suggested that populations are regulated during the winter when resources are scarce and that during the breeding season clutch size is determined by the resources available relative to the population density. Therefore, in habitats where seasonal fluctuation in food availability is high, mortality is also high in the winter, thus reducing the population density. When spring comes there is little competition for the abundant food supply and birds can easily produce large clutches. However, in those regions that experience little or only minor fluctuations in food availability, bird populations always remain near the habitat's carrying capacity. The competition for food during breeding is great and birds can only produce small clutches.

High density and food competition has been used to explain the small clutches of the New Zealand grey warbler (Gill 1982) and in European birds introduced into New Zealand (Niethammer 1970). This hypothesis may help to explain the brown creepers' small clutch size. If, as I have earlier suggested, New Zealand's coastal climate lacks strong seasonality, brown creeper populations would be near the carrying capacity of the habitat (i.e. K-selected) and competition for food great especially during the breeding season. Thus clutch size is reduced to adapt to the competition.

LENGTHS OF INCUBATION AND NESTLING PERIODS

The incubation and nestling periods of the brown creeper are long compared with those of northern hemisphere open nesting species. Lack (1948, 1954) suggested that the lengths of both the incubation and nestling periods are correlated with the security of the nest against predation. With few nest predators in New Zealand until recently, Lack's hypothesis may partially explain the brown creeper's long incubation and

nestling period.

GROWTH RATE

Ricklefs (1976) reported an average growth rate of 0.387 ± 0.079 for 30 tropical species in contrast to 51 temperate species which had an average growth rate of 0.502 ± 0.071. Thus, the slow growth rate of the brown creeper (0.353) is more similar to tropical than temperate species.

Ricklefs (1983) has recently argued that the variation in growth rate among bird species is related to the degree of maturity at fledging rather than such factors as juvenile mortality and food quality and availability. If this is true then brown creepers should fledge in a relatively mature state. This appears to be the case (see below).

MATURITY OF FLEDGLINGS

The maturity of nestlings and their rate of growth appear to be closely linked (Austin and Ricklefs 1977). Either nestlings develop slowly and fledge in a relatively mature state, as in the brown creeper, or they develop quickly but fledge in an immature state.

The degree of maturity of a nestling's various morphological structures before fledging seems to be guided by the principle of resource allocation to the growth of body parts with the highest functional priority (O'Connor 1977a,b). Thus, early growth and maturity of the tarsi in the brown creeper could be adaptive because they facilitate the development of the stretching and gaping response of chicks when parents arrive with food. In contrast, the delayed growth of the wings is possible because it is functionally unimportant to nestlings and permits the diversion of resources to meet more pressing needs. As much of the fledgling's first week out of the nest is spent perched

motionless in dense vegetation, avoiding predators, the complete growth of the wings can be delayed until well into the fledgling period.

PAIR-BONDS

Brown creepers formed prolonged monogamous pair-bonds. This is an unusual characteristic for small passerines because of their normally high annual adult mortality (Lack 1968). However, low annual adult mortality in the brown creeper makes permanent pair-bonds possible.

Prolonged pair-bonds may be advantageous for brown creepers because they maintain territories throughout the year. The cooperation of the two adults in the defense of a territory may be necessary outside as well as within the breeding season. During this study, I observed both members of pairs actively participating in territorial defense during the winter and the early stages of the breeding season. Furthermore, male and female male brown creepers each used specific vocalizations in territorial defense (Chapt. 6, p. 67-74).

DEMOGRAPHIC FACTORS

Reproductive Success

The reproductive success of brown creepers was similar to that found for two other species studied in Kowhai Bush. The hatching success of the New Zealand robin was 63%; breeding success, 26% and nestling success, 42% (Powlesland 1983). In the grey warbler, the hatching success was 69%, breeding success, 37.7% and nestling success, 54.1% (Gill 1982).

Late nests had a lower reproductive success than early nests. This trend was also reported by Gill (1982) for the grey warbler. Most brown creeper nest losses were due to predation by mustelids. King and

Moody (1982) have demonstrated that mustelids take more birds as prey in the summer than in the spring and that the majority of these are nestlings. Thus the difference in the reproductive success of late and early nests reported here probably reflects seasonal changes in mustelid diet.

Recruitment

The 10-11% recruitment rate of juvenile brown creepers into the breeding population was low when compared to the rate for three bird species in the northern hemisphere. Song sparrows (Melospiza melodia) and European blackbirds (Turdus merula) have an annual recruitment of 16% and great tits (Parus major),13% (Ricklefs 1973).

Survival of adults

Brown creepers had a low annual adult mortality (17.6%). Similar values have been reported in New Zealand for the robin (20%, Flack 1973) and the grey warbler (18.2%, Gill 1982). These figures contrast markedly with those of species in temperate-zones where annual adult mortality is 40-70% (Farner 1955). The mortality of adult New Zealand passerines is more similar to that for tropical-zone species which Ricklefs and Bloom (1977) found to be 10-30%.

Niethammer (1970) suggested that low adult mortality of New Zealand passerines is due to the relative lack of predators. This is probably also true of adult brown creepers because they spend most of their time in the canopy where they are difficult to capture by either mammalian or avian predators. A similar argument has been proposed by Gill (1982) to explain low adult mortality in the grey warbler. I think low mortality could also be related to the mild climate in coastal New Zealand. Starvation of adults would probably be unusual because the winter temperatures are mild enough to ensure readily available food resources.

BREEDING STRATEGY OF THE BROWN CREEPER

I suggest that the breeding strategy of the brown creeper is adapted to a mild climate in which food is available throughout the year. Because of stability in the food supply, the population may be near the carrying capacity of the habitat. Ashmole (1963) and Ricklefs (1980) have suggested that birds adapt to this type of habitat by producing small clutches. Cody (1966, 1971), in a similar hypothesis, suggested that by laying fewer eggs, birds in climatically stable habitats could devote more energy to other ways of increasing their fitness. One way appears to be increased egg size (Crowell and Rothstein 1981). For brown creepers, the laying of small clutches would allow more energy to be used to produce large eggs. The adaptive value in laying bigger eggs appears to be related to an increased survival rate of young hatched from these eggs (Skogland et al. 1952, Parson 1970, Schifferli 1973). The survival of young fledgling brown creepers is low so that there could be selective pressure on females to produce young which have the greatest probability of surviving to breed. I feel that the slow development of both embryo and nestling brown creepers is an adaptation to produce larger and more mature fledglings.

The overall breeding strategy of the brown creeper resembles that of tropical birds more closely than that of temperate species. However, there are some differences. In tropical birds, nestling growth rates are generally low (Ricklefs 1979, Oniki and Ricklefs 1981) but the selective pressures of high nest mortality in the tropics (Skutch 1967, Lack 1968, Ricklefs 1969b) have probably shortened the nestling period and caused the young to fledge immature (Ricklefs 1976). Tropical species have compensated for this by greatly extending the period of post-fledging care (Ricklefs 1969a, 1974). For example, Fogden (1972) found that in the tropical insectivorous species he studied, parental care

lasted 6-7 months. The brown creeper, in contrast, evolved in conditions of low nest predation where birds could remain in the nest for a long time and fledge in a relatively mature state. Because of New Zealand's mild climate and low degree of seasonal fluctuation in the levels of food resources, brown creeper population densities seem to be high and competition for food, mates and territories severe. This appears to be particularly true of young birds. Thus parents would be under selective pressure to produce offspring that could compete successfully. I suggest that in the brown creeper this is accomplished by producing large eggs and having slow nestling growth rate, thus producing mature young.

CHAPTER 5

THE SOCIAL ORGANIZATION OF BROWN CREEPERS IN THE NON-BREEDING SEASON

INTRODUCTION

Past studies on the social organization of birds outside the breeding season have concentrated primarily on describing the dominance relationships and aggressive interactions between individuals (e.g. Tordoff 1954, Kikkawa 1961, Brown 1963, Glaze 1973, and Ketterson 1979). However, information about the birds' dispersion and association patterns during the non-breeding season are also of great importance to understand the species social structure (Ficken et al. 1981). Herein I examine the organization of wintering brown creepers in Kowhai Bush by looking at their patterns of spacing and degrees of association.

Previously, Henderson (1977) had described several aspects of the brown creeper's non-breeding ecology. He found that the species commonly formed flocks of 5-8 birds in the autumn and winter. The cohesion of the flocks was highly variable and they occasionally divided into subflocks. The birds he studied showed low levels of intra- and interspecific aggression during the winter although after disturbances mobbing was common. The populations Henderson observed, however, were unbanded so he was unable to recognize individuals and determine precisely their social organization.

During my study of the communicatory behaviour of the brown creeper, it became clear that in order to facilitate the interpretation of these data more information was needed about the organization of the species during the non-breeding season. Using the banded population in Kowhai Bush, I attempted to answer the following questions: (1) Do all members of the study population flock in the non-breeding season? (2) Do all wintering birds show site fidelity or are some nomadic? (3) Do brown

creepers in the non-breeding season show any evidence of social structure (i.e. stable association patterns)?

RESULTS

SPACIAL ARRANGEMENTS

Adult members of the population in the main study area that had bred the previous season remained with their mates (see below) on their breeding territories and defended them against other pairs (Fig. 5.1). Defence in the non-breeding season entailed chasing and preforming "rapid" kee vocalizations (description of call, p. 74-75). Male song was only occasionally heard during the non-breeding season (Appendix 2).

In two cases, adult females who had lost their mates during the winter moved from their breeding territories. One of these paired with a male in another territory and the other disappeared. Six adult males who had also lost their mates all remained on their territories.

Birds that had fledged the previous season were less site-specific than adults and foraged over large portions of the study area (Fig. 5.2). The areas covered by young birds generally overlapped the territories of 2-4 adult pairs.

ASSOCIATIONS AMONG WINTERING BIRDS

I studied the associations among 20 brown creepers during the winter of 1980 and 19 birds in 1981 (see Table 5.1 for the colour-band combination, sex and previous history of each bird seen during the two non-breeding seasons).

Males and females who were paired during the previous breeding season associated closely with each other during the non-breeding season

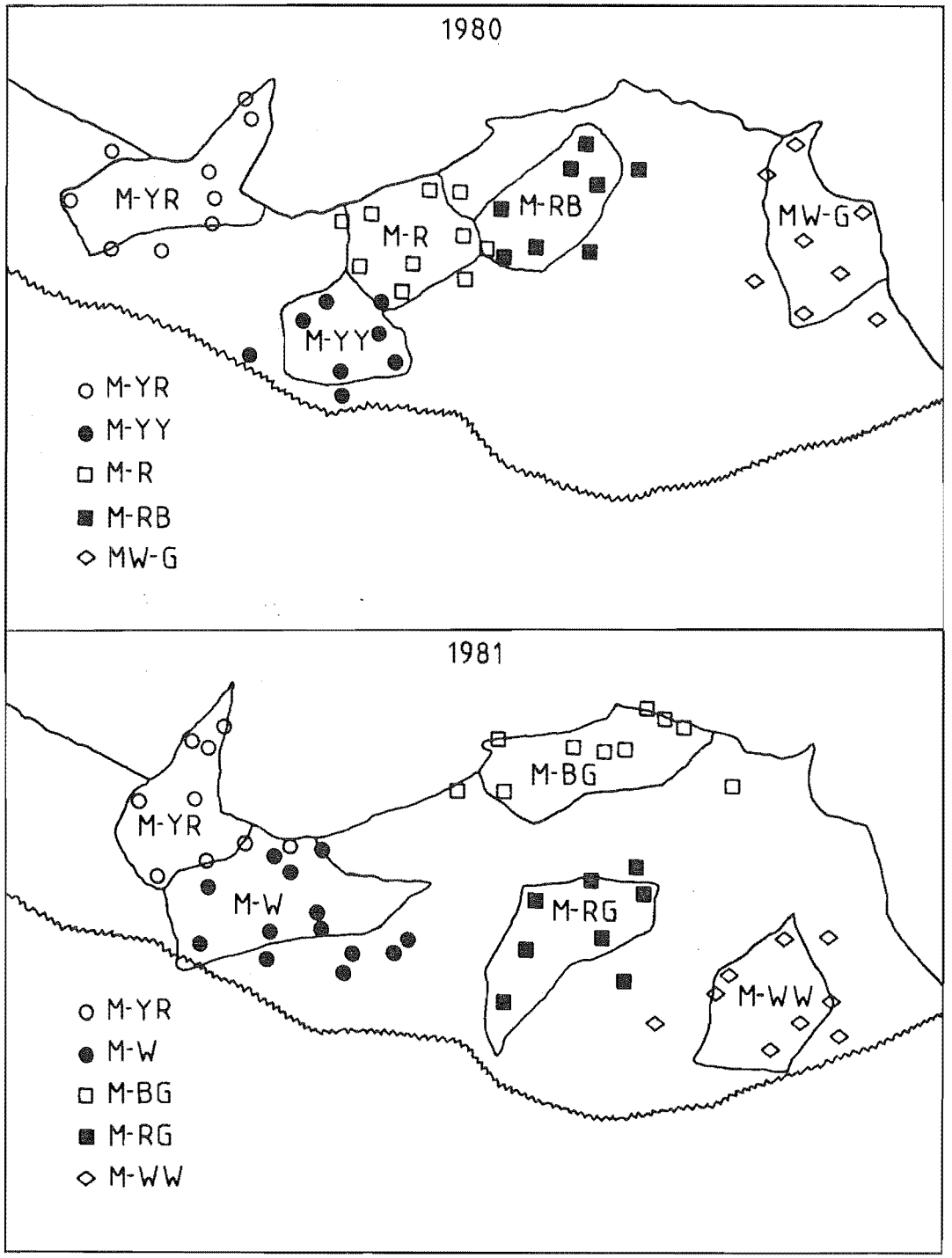

Fig. 5.1. Maps of the main study area showing where banded adult brown creepers were seen during the winters of 1980 and 1981 in relation to their territories of the previous breeding season. The letters indicate the birds' colour-band combinations.

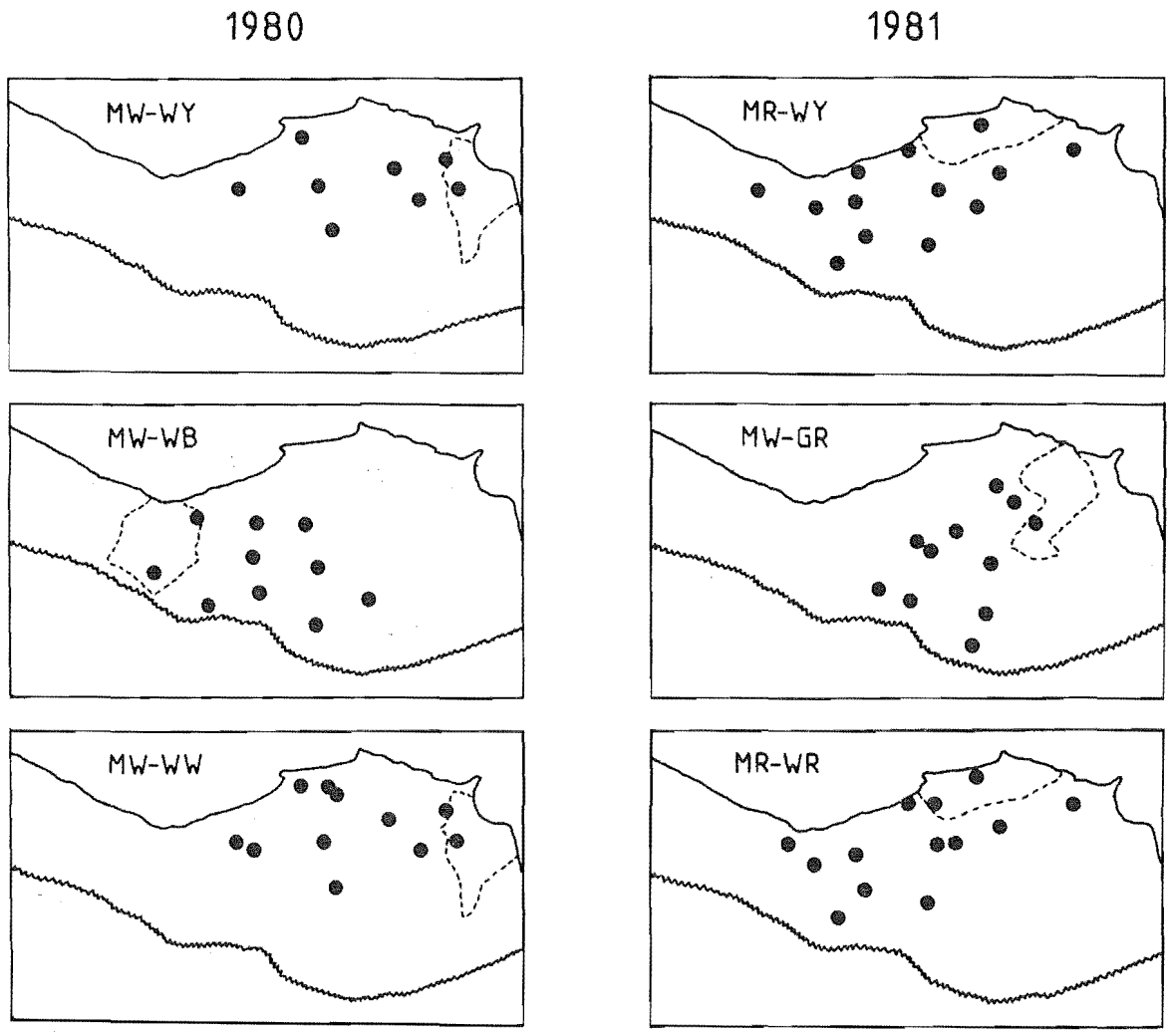

Fig. 5.2. Maps of the main study area showing sightings of 6 banded juvenile brown creepers in the winters of 1980 and 1981 (identified by band combinations). Their parents' territories are enclosed by dotted lines.

Table 5.1 Identification, sex and previous history of birds in main study area.

Colour-band code*	Sex	History
		1980
M-BG	♂	Paired with MY-Y
MY-Y	♀	
M-W	♂	Paired with unbanded female
M-RG	♀	Paired with M-YY
M-YY	♂	
M-YR	♂	Paired with M-GB
M-GB	♀	
MW-WW	?	Siblings; Parents MW-RG & MW-G
MW-WY	?	
MW-WG	?	
MW-BR	♀	Paired with M-WW
M-WW	♂	
MW-RG	♀	Paired with MW-G
MW-G	♂	
M-WB	♂	Paired with unbanded female
MW-WB	?	Siblings; Parents M-W & unbanded female
MW-RR	?	
M-R	♂	Paired with M-YW
M-YW	♀	
M-RB	♂	Paired with unbanded female
		1981
MW-G	♂	Paired with MW-RG
MW-RG	♀	
M-BG	♂	Paired with MY-Y
MY-Y	♀	
MR-WR	?	Siblings; Parents M-BG & MY-Y
MR-WY	?	
M-RG	♀	Paired with unbanded male
MW-YW	♂	Paired with unbanded female
MW-BG	?	Siblings; Parents MW-YW & unbanded female
MW-GR	?	
MR-R	♂	Paired with MW-WY
MW-WY	♀	
M-WW	♂	Paired with WW-BR
MW-BR	♀	
M-R	♂	Paired with M-YW
M-YW	♀	
M-YR	♂	Paired with unbanded female
MY-YR	♀	Paired with MR-WG
MR-WG	♂	

* See page 24 for interpretation of colour-band codes.

(Table 5.2A and B). For example, during observations in the winter of 1980, M-BG and his mate MY-Y were seen in association 48% of the time. No other bird spent as much time in close proximity to M-BG as MY-Y. Typically, during the winter, pair members were seen foraging together, often within 5 m, and if either bird flew off the other quickly followed.

Juvenile birds formed long-term alliances with nest siblings (Table 5.2A and B). For instance, MW-WW, MW-WR, MW-WY, and MW-WG fledged from the same nest on the 8 November 1979 and after leaving their parents, all four were seen together on the 20 February 1980. Three of them, MW-WW, MW-WR, and MW-WY were consistent companions between the 24 March 1980 and the 6 July 1980. Thus after fledging, these three birds had remained together for at least 8 months. In another case, MR-WR and MR-WY, who fledged on the 16 January 1981 were found associating for about 6 months, until 29 June 1981.

Other associative patterns also occurred but with much less frequency than those involving members of mated pairs or nest siblings. Adults were seen with their young especially with those that had fledged from late nests. In 1981, both MR-WR and MR-WY were with their father M-BG on seven and eight occasions, respectively. Adults also associated with young that were not their own; for instance during the winter of 1981, M-RG was found in close proximity to MW-BG on four occasions. These associations usually persisted only for the length of time the juveniles were within the adults' territories and when the young moved outside the boundaries the adult normally remained behind. Adults occasionally were found foraging close together with other adults; for instance, during 1980, M-BG was found with M-WB two times. Juveniles from different sibling flocks also joined each other in groups. On four occasions in 1980, MW-WW and MW-WB, members of different sibling flocks, were seen together.

Table 5.2A. Coincidence indices for birds during the winter 1980. Indices based on nearest associate observations.

	M-BG	MY-Y	M-W	M-RG	M-YR	M-GB	MW-WW	MW-WY	MW-BR	MW-RG	M-WB	MW-WB	MW-WG	M-R	M-YW	M-RB	M-YY	M-WW	MW-G	MW-RR
M-BG (20)[a]		0.49 (10)[b]*	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.10 (2)	0.0 (0)	0.0 (0)	0.13 (3)	0.09 (2)	0.15 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MY-Y (21)			0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.05 (1)	0.0 (0)	0.0 (0)	0.17 (4)	0.13 (3)	0.14 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
M-W (20)				0.0 (0)	0.0 (0)	0.0 (0)	0.09 (2)	0.09 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.21 (5)	0.05 (1)	0.13 (3)	0.09 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.24 (5)
M-RG (18)					0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.09 (2)	0.05 (1)	0.0 (0)	0.76 (14)*	0.0 (0)	0.0 (0)	0.05 (1)
M-YR (15)						0.52 (11)*	0.05 (1)	0.05 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.10 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
M-GB (27)							0.11 (3)	0.15 (4)	0.0 (0)	0.0 (0)	0.0 (0)	0.11 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.08 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.16 (4)
MW-WW (26)								0.31 (8)**	0.0 (0)	0.0 (0)	0.0 (0)	0.15 (4)	0.33 (8)**	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MW-WY (25)									0.0 (0)	0.0 (0)	0.0 (0)	0.12 (3)	0.26 (6)**	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.04 (1)
MW-BR (20)										0.0 (0)	0.15 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.10 (2)	0.0 (0)	0.62 (12)*	0.17 (3)	0.0 (0)
MW-RG (20)											0.20 (4)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.10 (2)	0.0 (0)	0.15 (3)	0.61 (11)*	0.0 (0)
M-WB (20)												0.04 (1)	0.05 (1)	0.0 (0)	0.0 (0)	0.15 (3)	0.0 (0)	0.15 (3)	0.06 (1)	0.05 (1)
MW-WB (27)													0.04 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.33 (8)**
MW-WG (22)														0.08 (2)	0.08 (2)	0.05 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
M-R (25)															0.36 (9)*	0.04 (1)	0.04 (1)	0.0 (0)	0.0 (0)	0.0 (0)
M-YW (25)																0.09 (2)	0.09 (2)	0.0 (0)	0.0 (0)	0.08 (2)
M-RB (21)																	0.10 (2)	0.0 (0)	0.0 (0)	0.0 (0)
M-YY (19)																		0.0 (0)	0.0 (0)	0.0 (0)
M-WW (19)																			0.06 (1)	0.0 (0)
MW-G (16)																				0.0 (0)
MW-RR (22)																				

a - total number of times each bird was counted as a nearest associate
b - number of nearest associate observations for each pair of birds
* - mated pairs
** - nest siblings

Table 5.2B. Coincidence indices for birds during the winter 1981. Indices based on nearest associate observations.

	MW-G	MW-RG	M-BG	MR-WR	MR-WY	M-RG	MW-YW	MW-BG	MR-R	MW-WY	M-WW	M-R	M-YR	M-YW	MW-GR	MW-BR	MY-Y	MY-YR	MR-WG
MW-G (27) [a]		0.68 (16) [b]*	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.15 (4)	0.0 (0)	0.0 (0)	0.0 (0)	0.17 (4)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.14 (3)	0.0 (0)	0.0 (0)	0.0 (0)
MW-RG (20)			0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.04 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.10 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.06 (1)	0.0 (0)	0.0 (0)	0.0 (0)
M-BG (27)				0.24 (7)	0.28 (8)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.43 (12)*	0.0 (0)	0.0 (0)
MR-WR (30)					0.33 (10)**	0.10 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.07 (2)	0.0 (0)	0.08 (2)	0.0 (0)	0.0 (0)	0.20 (6)	0.0 (0)	0.0 (0)
MR-WY (31)						0.13 (4)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.04 (1)	0.03 (1)	0.0 (0)	0.07 (2)	0.0 (0)	0.0 (0)	0.17 (5)	0.0 (0)	0.0 (0)
M-RG (29)							0.11 (3)	0.15 (4)	0.08 (2)	0.08 (2)	0.0 (0)	0.07 (2)	0.0 (0)	0.08 (2)	0.07 (2)	0.0 (0)	0.10 (3)	0.04 (1)	0.05 (1)
MW-YW (25)								0.21 (5)	0.14 (3)	0.09 (2)	0.0 (0)	0.07 (2)	0.0 (0)	0.0 (0)	0.20 (5)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MW-BG (23)									0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.57 (14)**	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MR-R (19)										0.53 (10)*	0.10 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.12 (2)	0.0 (0)	0.0 (0)	0.0 (0)
MW-WY (19)											0.15 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.12 (2)	0.0 (0)	0.0 (0)	0.0 (0)
M-WW (21)												0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.39 (7)*	0.0 (0)	0.05 (1)	0.06 (1)
M-R (29)													0.27 (5)	0.54 (14)*	0.0 (0)	0.0 (0)	0.10 (3)	0.0 (0)	0.0 (0)
M-YR (8)														0.19 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
M-YW (23)															0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MW-GR (26)																0.0 (0)	0.0 (0)	0.22 (5)	0.0 (0)
MW-BR (15)																	0.0 (0)	0.0 (0)	0.0 (0)
MY-Y (29)																		0.0 (0)	0.0 (0)
MY-YR (19)																			0.73 (12)*
MR-WG (14)																			

a - total number of times each bird was counted as a nearest associate
b - total of nearest associate observations for each pair of birds
* - mated pairs
** - nest siblings

DISCUSSION

Throughout the non-breeding season brown creeper pairs in Kowhai Bush remained on their breeding territories and defended them against other pairs. Brown (1964, 1969) has proposed that an animal should defend a territory as long as it is "economically defensible"; i.e., so long as the benefit of exclusive use of the area outweighs the cost of its defence. If this argument is correct, then brown creepers must be finding sufficient food within their territories to make it energetically profitable to exclude other pairs. This provides indirect evidence that food availability is relatively high throughout the year in coastal areas of New Zealand (see Chapt. 4).

Maintenance of a territory throughout the year may also increase the adults' efficiency at finding food because they would be more familiar with what is available on their territory. Other resources contained within the boundaries, such as water, shelter, and nesting and roosting sites would also be known.

Adult brown creepers may not be as sedentary in all habitats as they are in Kowhai Bush. If the cost/benefit ratio of resource defence is important in determining when a species will maintain a territory (Brown 1964), then non-breeding territories would not be found in habitats where food is scarce, unpredictable and unprofitable to defend. This might be true of brown creeper populations living at higher altitudes where, due to climatic conditions, food would be harder to find in the winter. At these high elevations all members of a population may be expected to form nomadic flocks.

In contrast to adults, the juveniles were less sedentary and foraged in flocks over large regions of the main study area. This raises an interesting question: Why do young birds become gregarious and form flocks in the non-breeding season? Pulliam and Millikan (1982) have

suggested that the costs and benefits of different forms of social organization determine the position on the continuum between territoriality and gregariousness that is taken by a particular bird.

Two major benefits of gregariousness have been proposed. Several authors have suggested that a bird in a flock is less likely to be surprised and taken by a predator than a solitary bird (Crook 1965, Goss-Custard 1970, Orians 1971, Pulliam 1973). This is presumably because in flocks there are more pairs of eyes available for seeing predators. However, because New Zealand may have had few predators before man's arrival, this was probably not the major selective force bringing about the evolution of flocking behaviour in the brown creeper. Furthermore, the primary predators of small New Zealand passerines, Australasian harriers and New Zealand falcons, hunt in open country (Fox 1977), and might be ineffective in dense forests. The other proposed benefit of flocking is its aid in the location and efficient exploitation of food (Short 1961, Morse 1970, Cody 1971, Murton et al. 1971, Krebs et al. 1972, Ward and Zahavi 1973, Pulliam and Millikan 1982). This comes about either through social facilitation, which Thorpe (1956) has defined as "contagious behaviour where the action of one animal may release identical behaviour in another", or local enhancement, whereby the attention of one individual is drawn to a particular location in the environment by the behaviour of another (Hinde 1959, 1961). Although I have no direct evidence supporting the hypothesis that juvenile brown creepers in flocks are more efficient at foraging than solitary ones, local enhancement behaviour was observed on numerous occasions within flocks of juveniles. In these cases, I saw birds quickly approach other flock members who had captured food and begin feeding nearby.

This study clearly demonstrates that in the non-breeding season strong associations exist between members of breeding pairs and also between siblings. The close association of members of pairs may simply

be a reflection of long term pair-bonds that are formed in this species (Chapter 4). At this time I can provide no explanation for the close bonds between siblings. However, the composition of flocks could have important implications for explaining the evolution of mobbing behaviour in the brown creeper.

It has been suggested that mobbing functions in alerting others to the presence of potential predators (Marler and Hamilton 1966, Sparks and Soper 1970, Kruuk 1972). If kin are more frequently warned than others and if mobbing individuals place themselves in jeopardy, kin selection could be important in understanding the evolution of mobbing behaviour (Curio 1978, Klump and Shalter 1984). In brown creepers, kin were present at all mobbing episodes which I observed during the non-breeding season but I never saw groups composed of unrelated birds mob (Appendix 1). Risks associated with mobbing have been documented for several species of birds (Hamilton 1964, Maynard Smith 1965, Dunford 1977, Hirth and McCullough 1977, Sherman 1977). Although I never saw a predator take a mobbing brown creeper it probably occurs since mobbing birds closely approach potential predators. In conclusion, I suggest that mobbing in the brown creeper has evolved through kin selection.

CHAPTER 6

COMMUNICATORY BEHAVIOUR OF THE BROWN CREEPER

INTRODUCTION

Investigations of the evolutionary pressures that have shaped the total display repertoires of species were pioneered by Smith (1969) and Moynihan (1970). Studies such as these, however, are few, presumably because the required observational data are time-consuming to gather and complex to analyse. On the other hand, if we are to begin to understand the relationship between communicatory behaviour and the social system it mediates, such studies must be undertaken. It was for this reason that I investigated the brown creeper's communicatory repertoire.

The aim of this study was to formally examine the communicatory behaviour of the brown creeper using W.J. Smith's (1969, 1977) semiotic approach. Using this approach, the information transmitted during communication and the evolutionary pressures responsible for shaping the complete display repertoire are examined. Information in this context is defined as an abstract property that permits choices to be made. There are three levels of investigation employed in semiotic theory; the first is syntactical and describes the physical properties of the signals (activities specialized for information transfer) used in communication; the information that is made available by a signal (semantics) is examined at the second level; and finally, the third or pragmatic level is mainly concerned with the value or usefulness of the information.

In the terminology used by Smith, the information encoded in the signal is defined as the message. Messages are determined in practice by noting the factors common to the situations in which signals occur and by considering the classes (sex, age, etc.) to which the communicators

belong (Smith 1968, 1977). The four general categories of messages may be defined as selectional, supplemental, identifying and locational (Smith 1977). Selectional messages are those that provide information about the communicator's intentions, while the likelihood or manner (partially or fully; weak or vigorous) in which this message will be performed is encoded in the supplemental messages. Signals also indicate the group (sex, age group, etc.) to which the caller belongs (identifiers) and the location of the communicator (locational). For a complete list of the messages contained in each of these four categories, see Smith (1977: 85-86). Each signal normally encodes several messages, including some from each category. Finally, the receiver's responses define the signal's meaning. Each signal may have one to several meanings and these are deduced by observing the responses of the receiver.

Smith (1977) envisions communication as an exchange of information which is beneficial for both the sender and receiver. Dawkins and Krebs (1978) have, however, convincingly argued that during communication it is advantageous, in most cases, for senders to manipulate or control the actions of the receiver. They suggest that signals should not evolve to provide "truthful" information to receivers but rather induce them by any means possible to behave in a way that benefits the sender. Receivers, on the other hand, should evolve the ability to use any information derived from the sender's acts to increase their own fitness (Wiley 1983). Thus manipulation in communication may work both ways.

Little was previously known about the communicatory behaviour of the brown creeper although a few vocalizations, used during the non-breeding season, had been verbally described by Henderson (1977). Thus, one of my principal goals in studying a free-living colour-banded population of brown creepers, was to identify and describe the total communicatory repertoire of the species. I also attempted to define the

information encoded in each signal and discuss the evolutionary pressures that have possibly shaped the species' communication system.

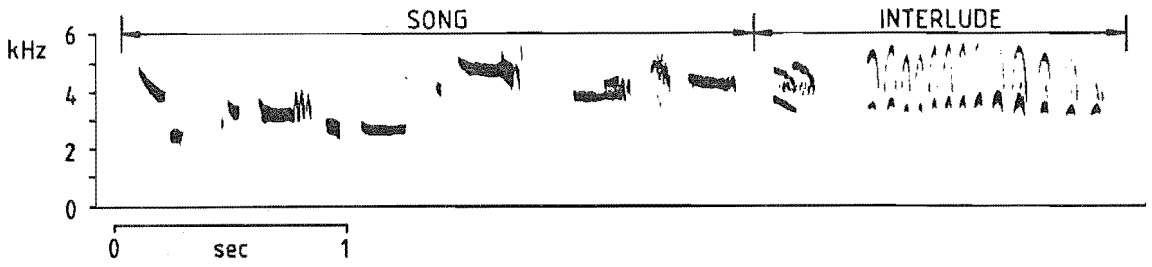

Fig. 6.1. Sonagram of the song and interlude of a male brown creeper recorded in Kowhai Bush.

RESULTS

VOCALIZATIONS OF ADULTS

The Songs of Males

The songs of male brown creepers were composed of loud sequences of slurs, whistles and harsh sounding notes ("song" in Fig. 6.1). Songs were 1.9-4.5 s long and composed of 5-14 notes which were 2.0-7.5 kHz in pitch. Most males sang only one song type which was stereotyped and individually distinctive (Chapt. 7). This vocalization will be referred to as male song.

Males had two singing performance patterns. In one, a string of 2-5 songs were sung, each song, often but not always, interconnected by what I have called interludes ("interlude" in Fig. 6.1). In this pattern of singing, bouts lasted 9.0 ± 2.31 s (n=10) with intervals between bouts of 20.2 ± 7.82 min (n=10). Males also sang single songs and in this case bouts were short (2.8 ± 0.81 s; n=11) with brief pauses between bouts (15.3 ± 1.82 s; n=11).

Male song was used primarily, if not exclusively, in territorial defense. On 10 separate occasions I observed that the singing activity of males who were setting up territories for the first time increased after they had begun defense. Before this, these males had not sung. In contrast, male song appeared to play little or no role in attracting a prospective mate. In two cases when males had lost their mates early in the breeding season both obtained new mates despite no increase in singing activity. Furthermore, males sang infrequently during the non-breeding season (March-August) (Appendix 2), the time when pair-bonds may be formed.

The two singing patterns described above were used in different contexts and different regions of the territory. Males sang strings of songs when patrolling the central portions of their territories or when responding to playback of song within their territories, but single songs were only used when males vocally interacted with neighbours along their boundaries. During these disputes the males frequently sang in unison (Chapt. 10).

A male's song undoubtedly contains information indicating the species, the sex and the individual identity of the singer (Chapt. 9). It may also encode the information that the performer is in possession of a territory, because males without territories did not sing. When there was no opportunity to interact with another male, such as occurs during patrolling, males sang strings of songs. This performance pattern may have encoded a message that the singer was seeking to interact socially with other males. A single song given when singing in unison may indicate that the communicator is attentive to the other interacting male with and is prepared to respond further (Chapt. 10).

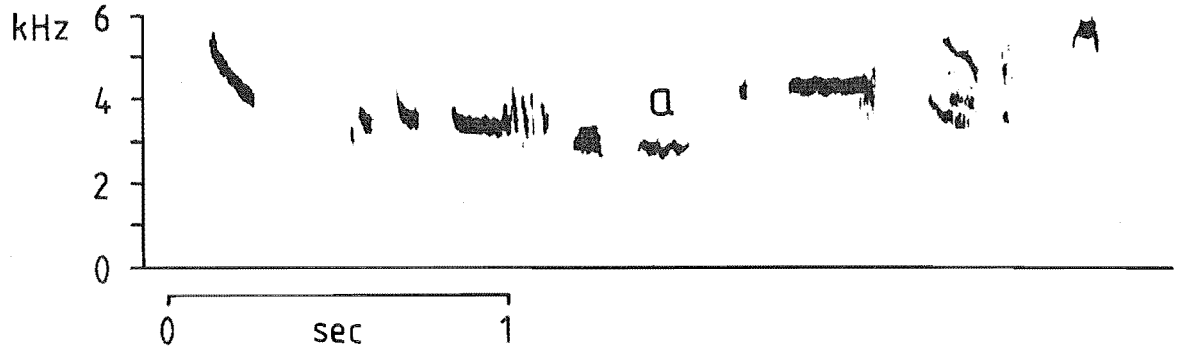

Fig. 6.2. Sonagram of a Kowhai Bush male's quiet song. The note labelled a shows frequency modulation and is characteristic of this male song variant.

Quiet Song

Quiet song was a variant of male song but, as the name implies, was sung at a lower volume (Fig. 6.2). All the males that were recorded singing quiet song also used male song at other times. Although quiet song was identical, except in intensity, to male song, the pitch of some notes wavered irregularly (element "a" in Fig. 6.2).

This song variant was heard on 10 occasions from young males who had just been attacked by a neighbouring male as they were setting up territories. The young males singing quiet song did not approach their attackers but remained several metres away.

Quiet song seems to imply that the singer is ready to interact but unlikely to attack or act agonistically towards his opponent.

The Songs of Females

Females sang differently from males. Their songs consisted of a rapid sequence of brief notes, the last of which was high pitched and slightly prolonged (Fig. 6.3A). The lengths of 20 songs were 0.8 ± 0.45 s, composed of 4–9 notes with a maximum frequency of 4.5 ± 0.11 kHz; and minimum frequency of 2.5 ± 0.12 kHz. All females sang only

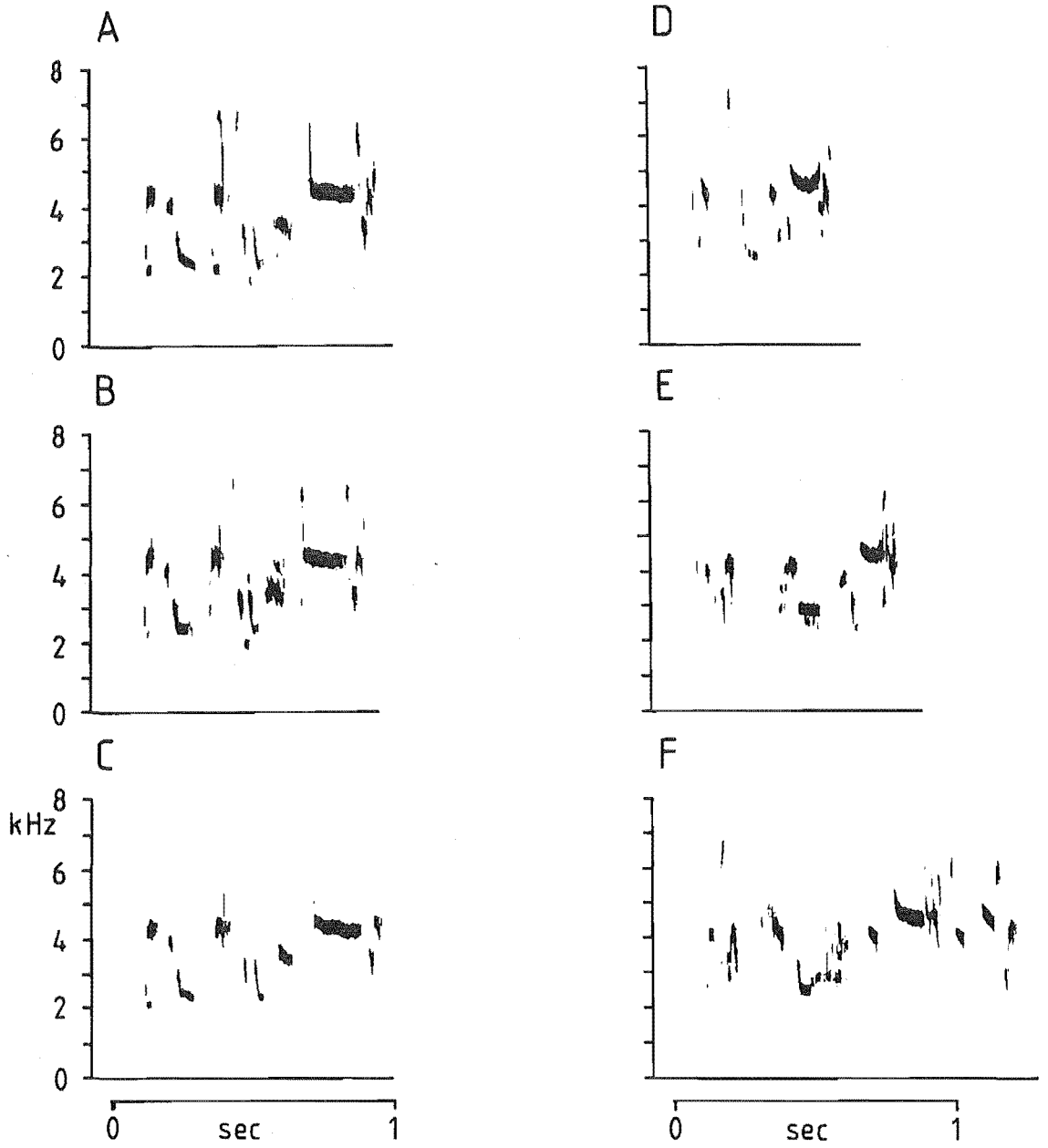

Fig. 6.3. A to C. Songs from one female in Kowhai Bush (note the uniformity in pattern). D to F. Songs of three other Kowhai Bush females.

one song type which was highly stereotyped (Fig. 6.3A-C). There were, however, great differences between the songs of individual females (Fig. 6.3C-F). The differences were primarily in the morphology of notes within the songs. The above vocalization will henceforth be referred to as female song.

Females sang frequently in solo or duets with their mates who sang male song (Fig. 6.4A). Songs of females were heard during both the non-breeding (April-August) and the early stages of the breeding season

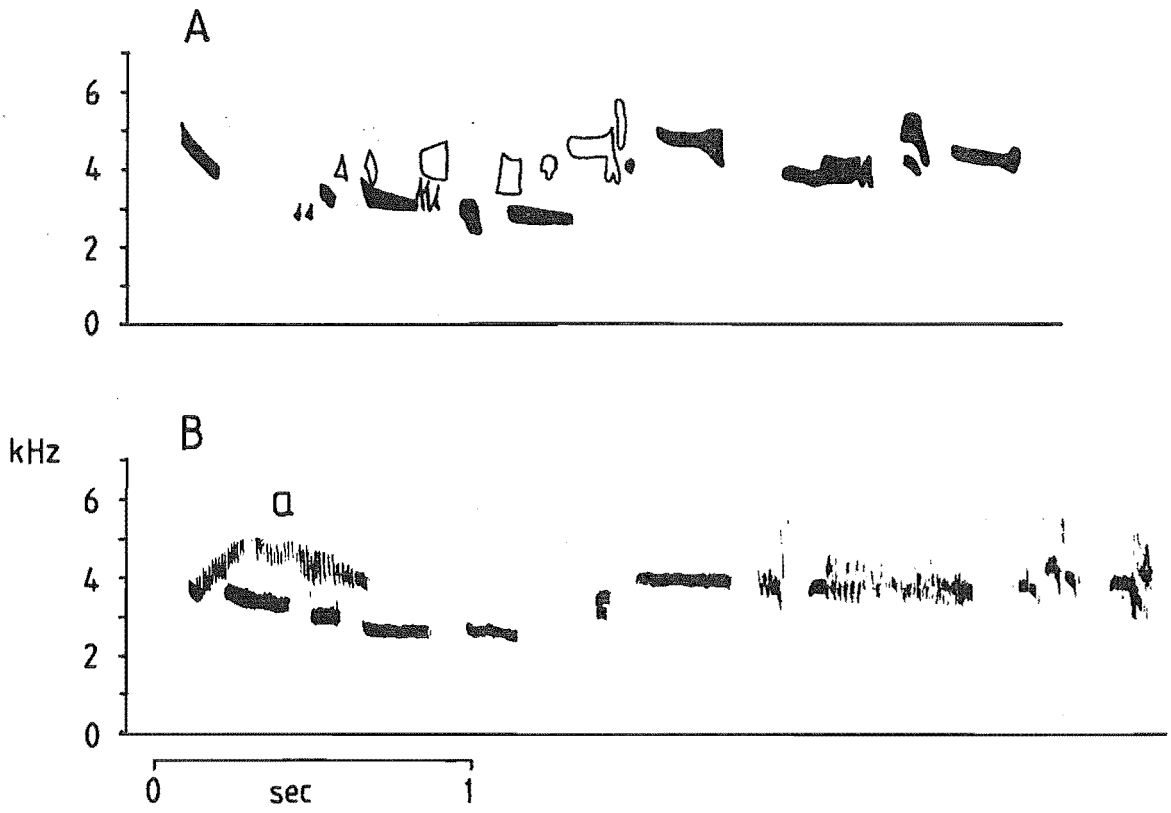

Fig. 6.4. Example of the two duet types performed by brown creeper pairs. A. Male song and female song duet from Kowhai Bush. Open figures are female song and solid ones male song. B. Male song and zeer duet from Freshwater Flat. Element a shows the female's zeer.

(September-October). I recorded 23 duets during the early stages of territorial disputes as the pairs approached their territorial boundaries. During the non-breeding season, 15 single females that were starting to associate with a male, and five other females temporarily separated from their mates, sang female song. On five other occasions, females whose mates were not nearby, sang when an intruder was discovered in their territory and the males all responded quickly by flying towards their mates. When I played a tape recording of male song to a paired female who was alone, she responded by repeatedly singing female song. Her mate soon joined her and began singing male song. Another female sang female song while she mobbed the observer, and although her mate was far off he quickly flew up and started to mob.

As in male song, the songs of females probably specify the species, sex and individual identity of the singer. In addition, female song appears to provide information that the singer is seeking to interact or associate with a mate or a prospective mate. Paired females used this vocalization, for example, to attract their mates for help to evict intruders or mob a potential predator. Females that were not paired, but which were associating with a male, possibly used female song to initiate interactions with their prospective mate and thus help establish pair-bonds.

Zeer

This call usually consisted of a single buzzy-sounding slur that began at 4.4 ± 0.08 kHz and descended to 2.8 ± 0.09 kHz (n=12) (Fig. 6.5A). One Stewart Island female produced zeers which on sonagrams had a short ascending tail at the start of the slur (element "a" in Fig. 6.4B). Zeers were 0.4 ± 0.01 s (n=12) in duration and composed of a series of sound impulses superimposed over several harmonics.

Only females who were with their mates and involved in a

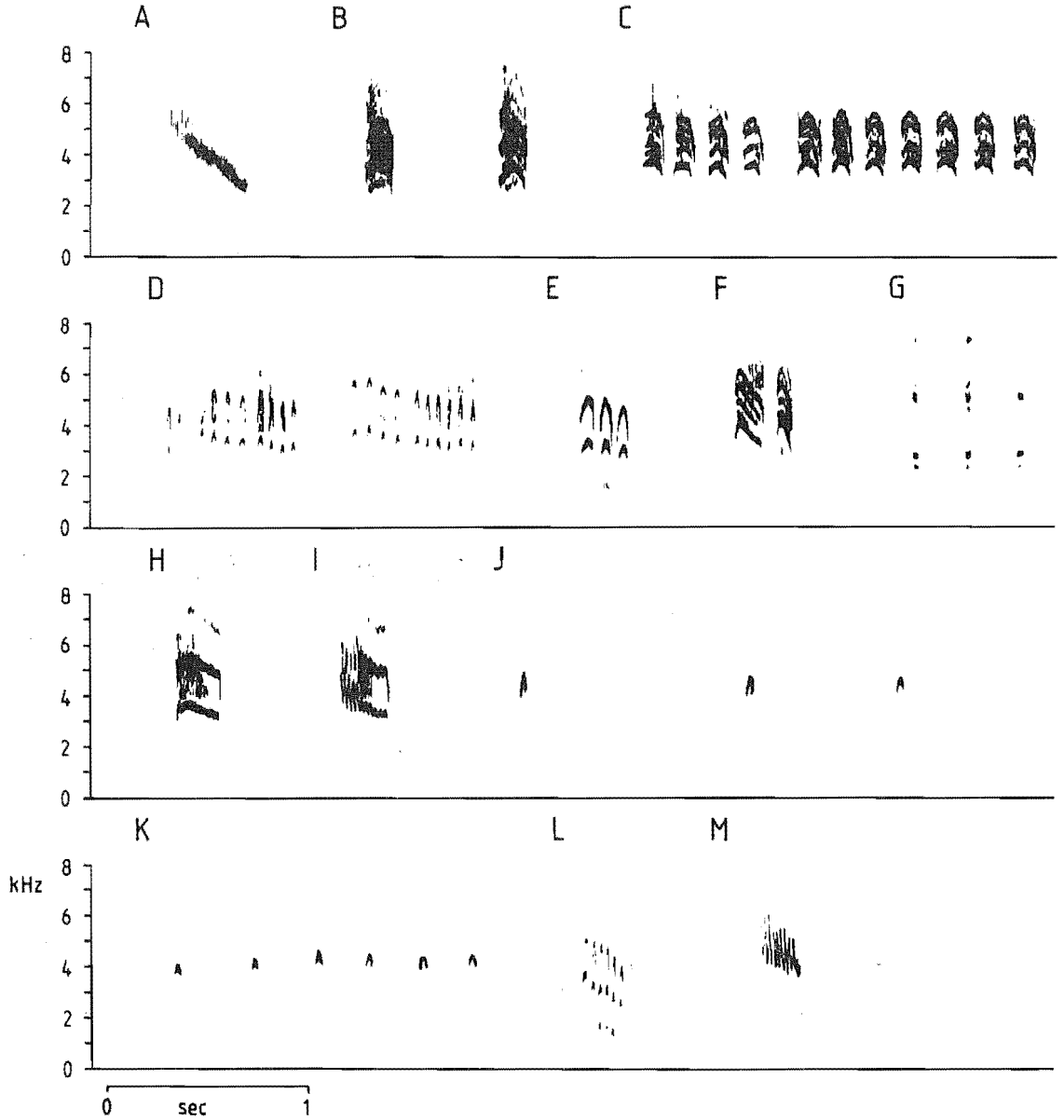

Fig. 6.5. Vocalizations of adult brown creepers. A. zeer, B. "slow" kee, C. "rapid" kee, D. chatter, E. tee-hee-hee, F. chee-cup, G. tick, H. chee, I. cheer, J. "slow" zick, K. "fast"zick, L. trill, M. zheep.

territorial dispute produced zeers. These were recorded on 31 occasions often when the caller was chasing a conspecific (n=20). Seventeen times the vocalization was performed as a solo while during the remaining 14, the callers used zeers in duets with mates who sang male song (Fig. 6.4B).

The message designated by the zeer seems to be that the caller is ready or going to attack or chase a conspecific. In addition, because members of pairs, when duetting, often timed their responses to each other's vocalizations in the same way each time, duets could identify mated pairs.

Kee

When shown in sonagrams, kees are flat chevrons composed of several closely stacked harmonics. Each chevron was 0.09 ± 0.001 s (n=20) in length and had a pitch of 4.2 ± 0.09 kHz. The number of kees given in a single bout varied greatly, but two temporal patterns of kee notes could be discerned: "slow" (Fig. 6.5B) and "rapid" (Fig. 6.5C). In "slow" kees, notes were separated by 0.15 ± 0.001 s (n=30) while the "rapid" ones were separated by 0.07 ± 0.013 s (n=50).

"Slow" kees were recorded on 49 occasions, 30 of which were probably in response to me standing or sitting motionless near a nest or a group of foraging birds. The call was given when parents responded to a fantail, grey warbler or silvereye foraging near a nest or fledged young (n=17). This call was also heard twice while parents chased their young who were persistently begging. In general "slow" kees were given by birds who, either alone or in pairs, approached the stimulus that had invoked the response.

The "rapid" kees were heard 35 times and in 25 of these the callers were mobbing either a cat, rat, stoat, New Zealand kingfisher (Halcyon sancta), shining cuckoo (Chrysococcyx lucidus) or the

observer. This call was also used during disputes between flocks or breeding pairs (n=10). Whenever "rapid" kees were used the callers approached the stimulus closely but unlike "slow" kees, the "rapid" calls were performed only by birds in groups composed of two or more individuals.

The caller or callers appeared to have had a strong attack tendency when giving the kee call. "Slow" and "rapid" kees might encode different probabilities of attack; the former encoding a lower one than the latter. Kees might be used to alert mates or flock members of important disputes or potential predators in the area.

Chatter

Chatters appear on sonagrams as a series of 3-15 simple chevron-shaped notes. Each note was 0.04 ± 0.006 s (n=20) long and was composed of several harmonics (Fig. 6.5D). The majority of the sound energy was between 3.2 ± 0.02 and 5.8 ± 0.05 kHz (n=20).

On 5 occasions, chatter was recorded from both males and females who were involved in pre-copulatory chasing and during four copulations only males gave the call. Chatter was commonly used by both sexes in unison singing bouts that included active chasing and physical fighting. It was also recorded from a pair which were responding to their nestlings flapping their wings, and from another that were watching their young fledge. In both cases when giving the chatter, the adults approached and then retreated from the young.

Chatter seemed to be performed when birds were trying to decide between associative behaviour (such as attack, copulation, or feeding) and escape behaviour. To female mates, the call may indicate that the caller poses no threat and that a bond-limited activity such as copulation may proceed. When given during territorial disputes, chatter probably suggests that a conflict exists in the caller between

attacking or retreating. This conflict is likely since most disputes occurred near territorial boundaries where there were no clear cut asymmetries such as ownership. Adults also chattered when their young moved within the nest or fledged. At this time, adults might have been uncertain about their offsprings' unusual actions and were not sure whether to approach and feed the young or stay away.

Tee-hee-hee

This call was composed of three chevron-shaped notes which were similar in structure, although the first was slightly longer (Fig. 6.5E). The notes contained two harmonics; one at 3.2 ± 0.02 kHz (n=21) and the other at 4.8 ± 0.02 kHz (n=21). The average duration of the entire call was 0.23 ± 0.008 s (n=21) with that of the first note, 0.08 ± 0.002 s (n=21), and each of the other two, 0.06 ± 0.001 s (n=21). The time interval between notes was 0.03 ± 0.005 s (n=15).

Both males and females were recorded using tee-hee-hee (n=15). In all these cases the caller was being attacked and displaced by either a conspecific or another species. Birds performing tee-hee-hee calls exhibited escape behaviour, usually by flying away or at least moving a short distance from the stimulus. Therefore, this vocalization probably conveys that the caller will move away from the attacker.

Chee-cup

Chee-cups, when analysed, were composed of two chevron notes skewed with long descending arms (Fig. 6.5F). Each note had two loud harmonics and several faint ones with frequencies of 3.2-6.0 kHz. The first note was 0.12 ± 0.02 s (n=12); the second 0.07 ± 0.007 s (n=12) with a mean interval between notes of 0.06 ± 0.009 s (n=12). Chee-cups were usually given singly but occasionally occurred in a series of 2-7 calls.

This vocalization, performed by both sexes, was recorded 14 times:

12 of which were during unison singing bouts. During unison singing, the callers approached and retreated from the birds they were interacting with while repeatedly giving chee-cups. This call was recorded once when a female was forced off the nest by her mate and in another case, when a female several times approached and moved away from her nestlings that were fledging.

Chee-cups probably encode a message of escape with a readiness to interact or associate thus providing information that the caller is undecided about what to do next.

Tick

The tick was a sharp mechanical-sound composed of two harmonics: one at 6.2 ± 0.12 and the other at 3.0 ± 0.10 kHz (n=10) (Fig. 6.5G). They were 0.02 ± 0.007 s (n=10) long and sometimes given singly but more frequently in a series of 2-6 notes.

Ticks were heard in apparent response to the presence of the observer (n=10) and once as a harrier flew over a female with fledglings. This vocalization was given only by females who were near their nest or their fledged young.

I heard this call only a few times and from just six individuals and I am uncertain of its message although it may include escape.

Chee

This note was a descending slur composed of two harmonics (Fig. 6.5H). The higher pitched harmonic began at 5.6 ± 0.07 kHz (n=20) and ended at 5.0 ± 0.06 kHz (n=20), while the lower began at 3.7 ± 0.04 kHz (n=20) and descended to 3.3 ± 0.05 kHz (n=20). Chee notes lasted 0.15 ± 0.015 s (n=25) and were usually given in a 2-4 note series.

I recorded this call on 30 occasions from foraging birds who were responding to my sudden appearance. The birds always stopped foraging and watched me but neither approached nor actively moved away from the

stimulus.

Recipients of this call were informed of the presence of a potential threat; one that should be kept under surveillance. Thus chees seem to encode a low intensity escape message.

Cheer

Cheers were similar in structure to chees except that the frequency was rapidly modulated giving the vocalization a rough buzzy quality (Fig. 6.5I). Often the modulations were more pronounced at the beginning of cheer notes.

Cheers were recorded on 14 occasions from both sexes. During 12 of these, adults gave the call as I attempted to capture their recently fledged young. Both the young and the adults actively retreated from me as they called. I also recorded the cheer as a flock of brown creepers were being chased by a New Zealand robin. Another time the young birds of a family group disappeared into thick vegetation when their parents gave this call as an Australasian harrier flew over.

Cheers may specify a stronger message of escape than chees. When chees were given, birds remained stationary, whereas, when hearing a cheer the birds actively retreated. The meaning of cheer calls might be "I am going to escape! Something dangerous is approaching!".

Zick

This vocalization was of short duration (0.05 ± 0.008 s; n=18) and composed of two harmonics; one at 2.0 ± 0.08 kHz and the other at 4.0 ± 0.09 kHz (n=17). Zicks were performed either slowly or quickly. In "slow" zicks (Fig. 6.5J), notes were unevenly spaced and the average internote interval lasted 0.42 ± 0.202 s (n=15) and during "quick" zicks (Fig. 6.5K) notes were more evenly spaced and the duration between notes was 0.25 ± 0.064 s (n=20).

Both "slow" and "quick" zicks were only given by birds who were

associating with a mate, nest siblings or other family members. In all the observed cases, possibly due to my presence, birds that had been foraging stopped, remained stationary and made this call (n=18). "Slow" zicks often changed abruptly into "quick" zicks if the callers flew away. "Quick" zicks were recorded on 12 separate occasions.

Zicks probably encode a message of associating behaviour helping to maintain the cohesion of groups or flocks during activities such as foraging or territorial fights. "Slow" zicks seem to help to reform a group of brown creepers that have separated, while "quick" zicks provide information that members should follow because the group is moving to a new location.

Trill

The trill consisted of a rapid series of 4-6 descending chevron notes each of which was composed of the second and third harmonics (Fig. 6.5L). The frequency of the second harmonic for 20 recorded trills began at 3.3 ± 0.04 kHz and ended at 2.8 ± 0.04 kHz while the third started at 4.9 ± 0.03 kHz and descended to 4.1 ± 0.02 kHz. Trills lasted 0.21 ± 0.057 s (n=20).

Trills were only recorded during unison singing bouts, just before songs that were sung in unison. This vocalization was only recorded from males.

The information encoded in the trill seems to be that the caller is about to sing. It could be used to capture the attention of the receiver during vocal interactions. Trills may thus function as an alerting signal (see Wiley 1983, Wiley and Richards 1982). This hypothesis is only tentative, however, as I could not be certain as to which of the two males unison singing males actually made the call.

Zheep

The zheep was a simple buzz that descended in pitch from 5.6 ± 0.15 kHz to 4.3 ± 0.10 kHz (Fig. 6.5M). The modulation rate of this call was ca. 50 Hz.

Zheeps were recorded only from adult females (n=5). On three of these occasions callers were attempting to obtain food from their mates. Copulation immediately followed the performance of zheeps in the other two cases. Wing flutter was always used in conjunction with this vocalization.

This call probably indicates that the communicator is ready to accept bond-limited receptive behaviour such as courtship feeding or copulation. However, the kind of behaviour to which the caller is receptive is not specified.

VOCALIZATIONS OF THE YOUNG

Buzz

This vocalization was similar to the zheep except that it was higher in pitch (9.1 ± 0.35 kHz) (Fig. 6.6A). Its modulation rate was ca. 63 Hz. The length of the call was highly variable and appeared to depend to a large extent on how quickly parents responded to young making the sound.

This vocalization was recorded on over 50 occasions. It was given by both nestlings and fledglings attempting to obtain food from parents. Two to three day old nestlings began giving the call and continued to produce it for several days after fledging and although there was no observable structural change during that time, the call did become louder as the young matured. During the first week after hatching, a buzz could only be heard within 1-2 m of the nest but just before fledging it was audible 6-7 m away. The young birds always performed wing flutter

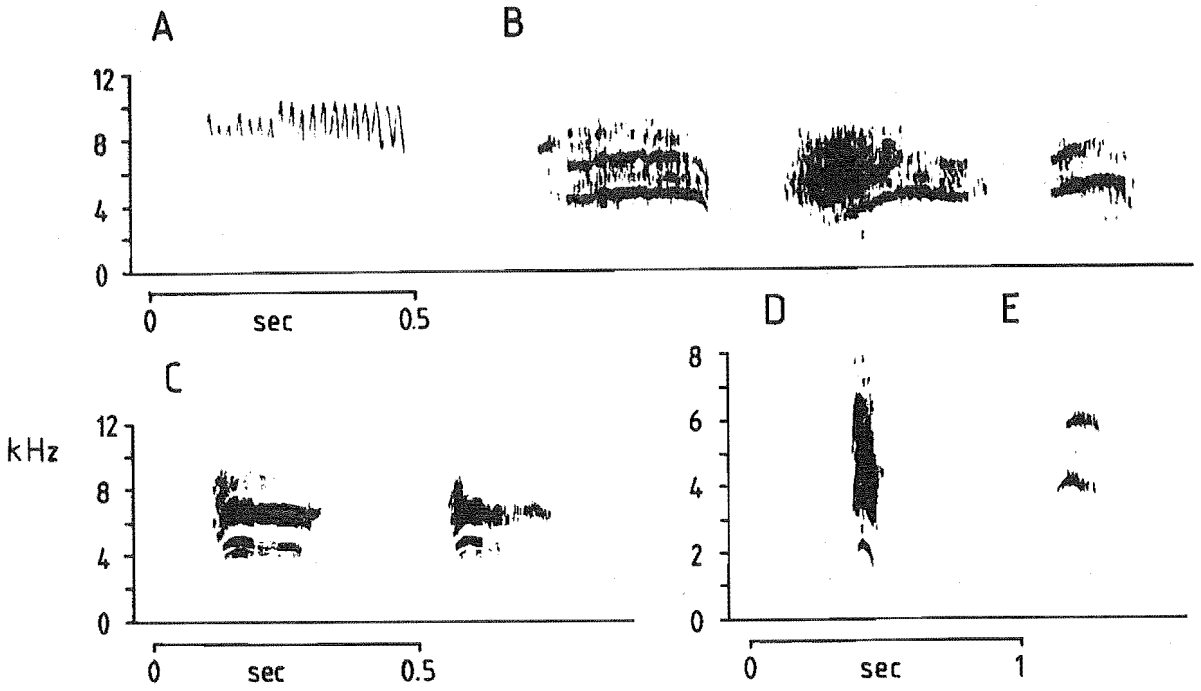

Fig. 6.6. Vocalizations of nestling and fledgling brown creepers. A. buzz, B. zee, C. skree, D. chip, E. see.

with this call.

The message encoded in the buzz is probably that the caller is seeking care behaviour (feeding). The meaning to parents would be "Approach the caller and feed it".

Zee

Zees, shown as long flat chevrons, in sonagrams, were composed of several stacked harmonics that produced a harsh sound (Fig. 6.6B). Each note was 0.27 ± 0.10 s (n=20) with most of the sound energy concentrated at 4.4 ± 0.13 kHz (n=15).

Zees were produced by fledglings that had been out of the nest for at least 1 week and were attempting to obtain food from parents (n=35). They were also performed in late autumn and early winter by four young birds when they were attacked and chased by parents. In 20 cases, wing flutter accompanied the performance of zees.

Zees appear to provide information that the communicator is prepared to accept care such as feeding from parents. Furthermore, because young gave the call when being attacked and chased by parents, it could also encode a message that the caller was ready to interact or associate with the aggressor in a non-aggressive way.

Skree

When analysed, skrees, were asymmetric round-topped chevrons with long descending tails (Fig. 6.6C). Each note lasted 0.17 ± 0.03 s (n=20) and had a pitch of 6.7 ± 0.23 kHz (n=10). The sound had a rough quality created by the closely stacked harmonics.

This call was recorded on 14 occasions and was only produced by nestlings or fledglings that I was handling. The skree seems to be an expression of a thwarted escape tendency and indicate that the caller is seeking escape from a predator. Parents responded to skrees by mobbing, giving "rapid" kees and performing the wing-up display. These reactions from adults might allow escape of the victim by diverting the attention of the predator.

Chip and See

The chip was brief in duration (0.05 ± 0.004 s; n=10) and, when analysed in sonagrams, is chevron-shaped (Fig. 6.6D). It covered a wide range of frequencies (2.0-7.0 kHz) and was only given singly. Chips were heard or recorded on 15 occasions from fledglings that may have been out of visual contact with their parents. The callers were usually motionless and in very dense vegetation.

Sees were slurs composed of two harmonics (Fig. 6.6E). The majority of the sound energy was concentrated at 6.2 ± 0.34 kHz (n=9) and frequency was modulated irregularly throughout the note's 0.15 ± 0.03 s.

I recorded sees five times from nestlings that had fallen out of

their nests. The birds were presumably hidden in thick cover away from their parents' view.

Chips and sees seem to be used by young when they need feeding or other forms of care, and are attempting to obtain contact with parents. Thus, the general message is that the caller is seeking attention in the form of food or association with parents. Parents always responded to these calls by assuming the search posture (Fig. 6.8C). Chips and sees might also provide locational information since they are both composed of a wide range of frequencies that provide abundant cues for locating the source of the sound (Marler 1955).

GRADED SIGNALS

Several of the vocalizations, previously described, graded into one another. The following are descriptions of these graded sequences.

Chatter graded into kee (Fig. 6.7A) - This was recorded on three occasions during which the caller was approached by another conspecific. The bird remained several metres away from the approaching conspecific and performed chatter, however, as chatters graded into kees, the caller quickly approached and chased the other bird away. Thus, at the beginning of the sequence each caller might have been hesitant about interacting with the approaching bird but then recognized it as an intruder and attacked.

Chee graded into cheer (Fig. 6.7B) - Both chees and cheers encode a message of escape but they seem to differ in the intensity of the response. In both cases where this sequence was recorded the callers were within family groups that were probably reacting to my presence. When giving the chee, the birds remained stationary but attentive to

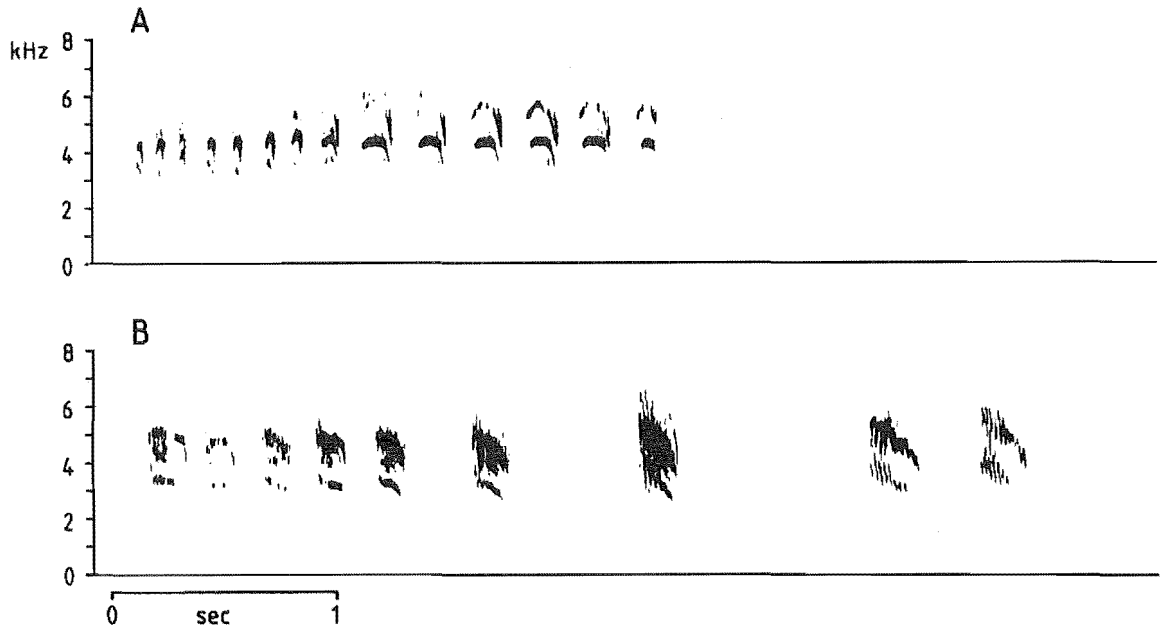

Fig. 6.7. Graded adult vocalizations. A. chatter graded into kee, B. chee graded into cheer.

the stimulus and with my continued approach, the calls were graded into cheers and they moved away from me. Thus this sequence may encode a graduated change in the intensity of the escape message.

NON-VOCAL DISPLAYS

Singing Postures

When singing strings of songs, males assumed an upright posture (Fig. 6.8A). The tail, not usually spread, was held directly below the body while the bill pointed forward. The crown and throat feathers as well as those on the body were erect. While singing, males pivoted on their feet scribing an arc of ca. 45-90°.

While performing single songs during vocal interactions, males maintained a different stance. They kept their bodies approximately parallel to the perch and sleeked their crown, throat and body feathers (Fig. 6.8B), occasionally, they spreading their tails and fluttering

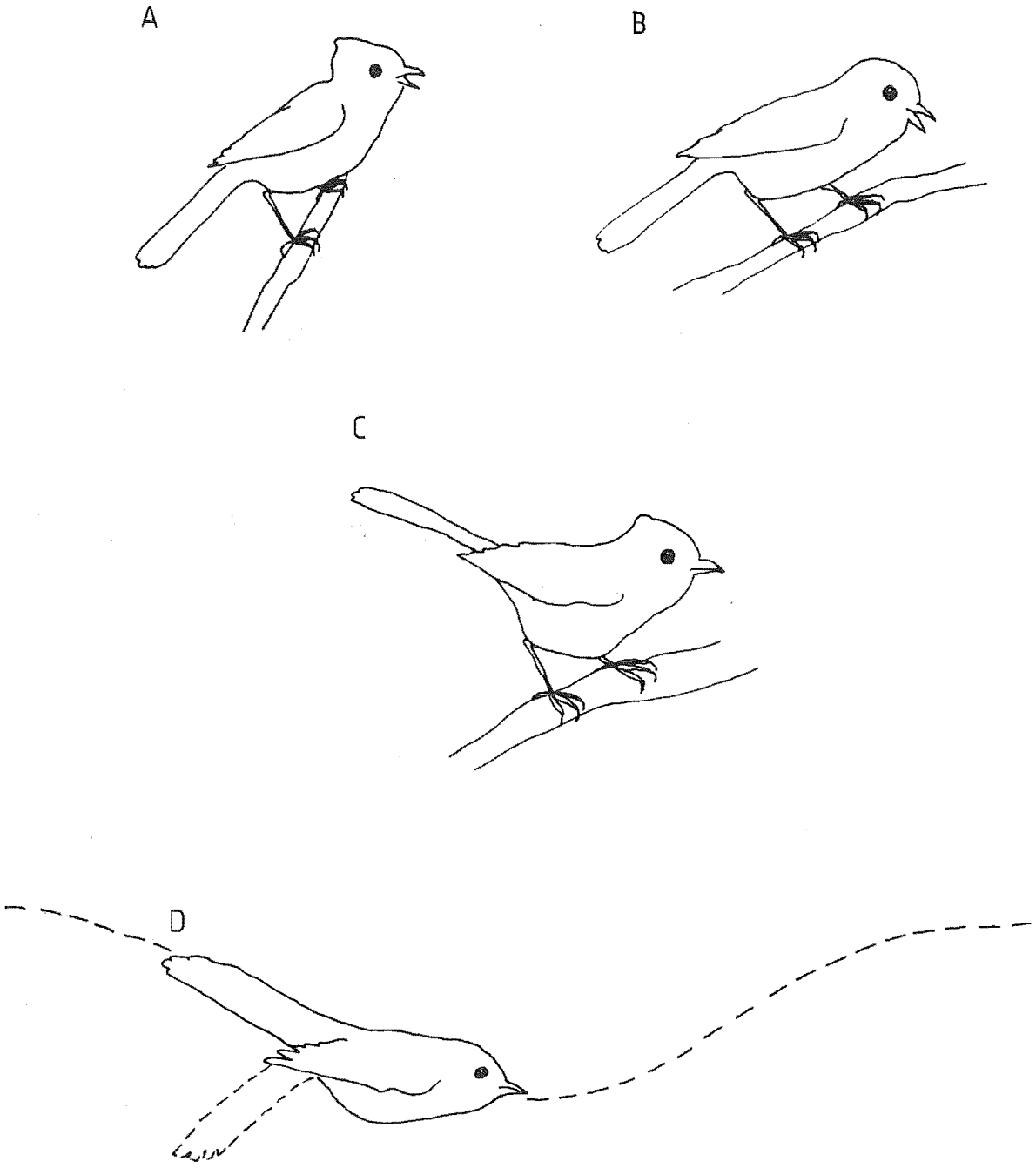

Fig. 6.8. Some visual displays of adult male and female brown creepers. A. singing posture when singing alone or in centre of territory (note the raised crown feathers and head held up), B. singing posture when singing in unison (note sleeked crown feathers and lowered head), C. searching posture, D. undulating flight.

their wings. When unison singing, their bodies were oriented so that the bill pointed towards the other bird.

The messages encoded in these two postures were probably similar to those of the vocalizations performed when assuming them.

Searching Posture

When adopting the searching posture, brown creepers hopped quickly about from branch to branch appearing to examine their surroundings (Fig. 6.8C). Their necks were fully extended, the crown and throat feathers erect, and the unspread tail, which was flicked frequently, held at an angle of 15–20° above the horizontal axis of the body.

This posture was used by both males and females when approaching territorial intruders that had not yet been seen. It was also used by males as they guarded their mates during the early stages of the breeding cycle (Chapt. 4, pp. 28–29). Both sexes assumed the searching posture when looking for young that were making chips or sees.

The searching posture probably visually informs others that the performer is attentive to a stimulus (a singing male, a mate or a calling young) and that it is prepared to respond further to that stimulus. The form of the response is not specified since it could either attack a trespassing male or provide food to an offspring.

Undulating Flight

During normal flight, the path followed by brown creepers was only slightly undulating. Undulating flight, in contrast, appeared extremely laboured and slow. The bird's crown and throat feathers were erect and the tail was spread and flicked from 15–20° below to 15–20° above the horizontal (Fig. 6.8D). Normal flight usually took place in dense vegetation but birds performing undulating flight flew back and forth across openings in the forest. When the tail is spread, dark brown

patches on the tail formed a conspicuous band which could be seen when birds were performing this display.

Undulating flight seems to indicate that the birds are seeking to attack or interact with an intruder. The performer probably attempts to make itself as conspicuous as possible so that intruders will see it.

Wing-up Display

In this display, the wings were partially extended and held above the back in a broad "v" shape as if the bird was about to fly (not figured). While holding its wings in this position, the bird appeared to lean forward, hopping from perch to perch and moving around the observer, often at very close range. The bird's crown as well as throat and breast feathers were erect and the spread tail was flicked frequently. "Rapid" kees always accompanied this display.

The wing-up display was observed on 18 occasions, 14 of which occurred when adults responded to skrees from their young. I saw this behaviour three times given by adults who were with fledglings, possibly in response to my pierced-lips-squeeks. The display was also given once by a female as I was approaching her nestlings.

This display might represent a ritualization of movements associated with taking flight indicating a tendency of the performer to escape. Since wing-up always occurred in association with "rapid" kees it could specify that the bird is experiencing a conflict between attacking or escaping a potential predator.

Wing Flutter

The wing flutter consisted of the synchronous beating of half-extended and slightly raised wings. During this display the bird assumed a crouching posture (see below), stretched its wrists only slightly to the sides and extended its primaries backward.

Wing flutter was performed by females soliciting food or

copulation from mates and by young trying to obtain food from parents. This display was also observed during territorial disputes and was given by young males, females or males who had been chased. Thus, the message encoded is probably that the caller was ready to accept copulation, care-giving or associative behaviour from the receiver and was unlikely to attack.

Crouching Posture

The crouching posture was assumed by both females and fledglings when begging for food and by females just before copulation. The bird lowered its body to the feet, pulled its head towards the body and oriented its bill toward the receiver. The wing flutter, and zheep, buzz or zee calls were also associated with this posture.

When given by paired females, this crouch probably specified that the female was ready for receptive behaviour such as courtship feeding or copulation and when performed by young birds it indicated that they were seeking parental care or receptive behaviour like feeding.

DISCUSSION

The communicatory repertoire of the brown creeper consisted of a total of 26 displays; 19 vocal and seven visual. There may be more visual displays but it was difficult to get close enough to observe the subtle details of visual displays because of dense vegetation. Most social species of vertebrates are limited to repertoires of 15-40 displays (Smith 1969, 1977; Moynihan 1970). This relatively small number of displays may result from selective pressures against both heterogeneity and unchecked multiplication (Moynihan 1970). Moynihan suggests that as the number of displays increases, each new display must be more distinct from the others; however, the degree to which displays

can be elaborated are limited. These limits are caused by constraints on the length of time a sender can spend performing the display and the amount of time a receiver must spend attempting to distinguish the display from others. An overly elaborate display could be too conspicuous and attract the interest of predators or competitors (Moynihan 1970).

Several brown creeper displays encode the same selectional message and thus appear to be redundant (Table 6.1). These displays, however, probably differ in the supplemental messages they specify (i.e. they may vary in the probability that the caller will undertake a specified activity). For example, there are ten displays indicating the escape message, varying from a weak tendency in chee-cup to a strong one in cheer or tee-hee-hee. These relatively fine differences in the probability of escape would be useful to persistently social species, such as the brown creeper, because of changes that occur in the social relationships between birds due to experience from earlier encounters with the same individual or seasonal variation.

Three specific attributes of the communicatory repertoire and the selective forces which may have shaped them are worthy of discussion. First, each male brown creeper possesses only a single song type; but this song type is performed in two distinct manners. Single songs are used with neighbours during social interactions on territorial boundaries. Strings of songs are sung by birds who are alone and patrolling their territories.

I suggest that male brown creepers, because they possess only one song type, must vary the performance of their song in order to communicate different messages such as different levels of attack probability. In at least three-quarters of all song bird species, males sing more than one song type (Hartshorne 1973, Dobson and Lemon 1975). In several of these species it has been demonstrated that song types encode different messages (Ficken and Ficken 1965, 1966; Morse 1966,

Table 6.1 Brown creeper vocal and visual displays and the messages they encode.

	Interactional	Attack	Escape	Copulation	Association	Indecision	Locomotory	Behaviour of remaining w/site	Seeking	Receptive	Attentive
Male song	X	X	X		X			X	X		
Quiet song	X		X		X				X		
Female song	X				X				X		
Zeer			X								
Kee		X	X								
Chatter		X	X	X	X						
Tee-Hee-Hee			X								
Chee-cup			X								
Tick			X		X						
Chee			X								
Cheer			X								
Zick					X		X				
Trill									X		X
Zheep	X			X	X					X	
Buzz	X									X	
Zee	X									X	
Shree			X						X		
Chip					X				X	X	
See					X				X	X	
Singing Posture 1	X	X			X			X	X		
Singing Posture 2	X	X	X		X			X	X		
Searching Posture									X		X
Undulating Flight		X							X		
Wing-up			X			X					
Wing Flutter				X						X	
Crouch				X						X	

1967, 1970; Lein 1972, 1978; Smith et al. 1978). For example, Lein (1978) has shown that in the chestnut-sided warbler (Dendroica pensylvanica), three of the species' song types are sung in the centres of territories where attack is likely while the other three are only sung on the boundaries where attack and escape tendencies are more or less balanced. Even without a varied song repertoire, the brown creeper is still confronted with similar selective pressures for efficient maintenance of boundaries and probably uses the two singing performance patterns to accomplish this. A similar argument has been put forward by Rich (1983) to explain the partial and complete songs used by the sage sparrow (Amphispiza belli); a species that also sings only one song type. Rich has proposed that incomplete songs may be used in conditions of increased stimulation, coupled with uncertainty of attack while complete songs are sung when attack is more likely.

The second point to be discussed is that males and female brown creepers duet. Year-round territoriality and prolonged monogamous pair-bonds are two characteristics common to a majority of species which duet. These tendencies may be responsible for the evolution of duetting in these birds (Farabaugh 1982) and may also have been important selective forces fostering duetting in the brown creeper. Bird species maintaining year-round territories inhabit regions that experience only minor changes in the abundance of food between the breeding and non-breeding seasons (Farabaugh 1982). Such areas may not provide sufficient resources to support more than one nesting female in a territory and thus, females would be under selective pressure to defend their territories against other females. Farabaugh suggests that this favours the development of song in females. She also proposes that coordination in territorial defense is advantageous and duetting would be a way of organising offense against other conspecific pairs and reducing the possibility of misdirected aggression towards a mate. Farabaugh

suggests that duetting functions in the development and maintenance of long-term pair bonds and could be a fundamental phase in its formative process. Such bonds could aid in the defense of a territory because rivals may be less likely to intrude into a territory defended by two birds.

Earlier I proposed that coastal regions of New Zealand experience little variation in food availability throughout the year and that this has favoured the evolution of year-round territoriality in the brown creeper (Chapt. 4 and 5). If this is true, then as Farabaugh suggests, it would be profitable for females to participate in territorial defense by keeping out other females. During this study I often saw females chase neighbouring females out their territories during disputes (Chapt. 4, p. 38).

Duets seem to have several functions. Among these are coordinated defense of territories, maintenance of pair-bonds and synchronization of sexual behaviour (Thorpe and North 1965; Hooker and Hooker 1969; Todt 1970b, 1975; Thorpe 1972; Wickler 1974, 1980; Baptista 1978; Wickler and Seibt 1980; von Helversen 1980). In the majority of duetting species, pairs have only one duet type and this serves several of these functions. I found, however, that the brown creeper has two duet types, one used in territorial defense and the other in male-female interactions. Baptista (1978) has also described two duets in the Cuban grassquit's (Tiaris canora) repertoire; the first employed in territorial and the other during sexual interactions.

The third point to note is that brown creepers use graded signals. This finding departs from the commonly held view that most bird vocalizations are discrete (with no intermediate forms) (Marler 1967; Smith 1968, 1969). I suggest that brown creepers use graded signals because they provide a more refined and subtle way to communicate changes

in motivational states. Marler (1967, 1973) has argued that graded signals are employed by species communicating at close range. Under these circumstances, the signal would not be distorted by environmental attenuation between the sender and receiver, allowing the intermediate forms of the signals in the graded sequence to be identified. I found that most interactions between brown creepers occurred over short distances, allowing graded signals to be employed.

I also noted in this study that graded signals were performed in rapid series. Marler and Tenaza (1977) have suggested that a correlation exists between the degree of vocal grading and the tendency for the signal to be uttered in strings. They argue that the amount of change and the direction of a signal can be more readily assessed by the receiver when the signal is performed in strings.

CHAPTER 7

SONG DEVELOPMENT AND VARIATION IN THE BROWN CREEPER

INTRODUCTION

The songs of many bird species have been found to vary geographically (review: Krebs and Kroodsma 1980). This variation often involves differences in the occurrence, structure or sequence of song elements; in the type of songs used; or in the size of song repertoires. Songs may vary in a continuous clinal manner or, alternatively song dialects may exist among groups of neighbouring birds who sing similar songs which differ more or less abruptly from those sung by more distant groups (Marler and Tamura 1962, Thielke 1969, Mundinger 1975).

Three major hypotheses or models have been proposed to explain the origin and adaptive significance of song dialects in birds: 1) historical, 2) racial specialization and 3) social adaptation (Marler and Tamura 1962, Nottebohm 1975, Baker and Mewaldt 1978, Payne 1978).

According to the historical hypothesis, song dialects develop through the accumulation of small changes in the song patterns of birds in isolated populations and have no adaptive significance. Because many species of song birds learn their songs, changes in their songs result from errors in song development (Lemon 1971, Baptista 1972); improvisations of parts of songs (Marler and Tamura 1964, Marler 1970); or inadequate instruction during song learning (Baptista 1975, Baptista and Johnson 1982). The historical model has been used to explain the development of song dialects in a number of bird species (Thielcke 1969, 1973; King 1972; Baker 1975; Baptista 1975, 1977).

The racial specialization model was first proposed in detail by Nottebohm (1972) and has been widely cited to explain the adaptive significance of dialects in a number of species (Marler and Tamura 1962;

Nottebohm 1969; Thielcke 1970; King 1972; Baker 1974, 1975). It argues that populations of birds become genetically specialized to local environments and that song dialects are employed to indicate an individual's membership in a particular population. A bird's specialization to local conditions would result from past natural selection and differences in song patterns caused by random changes in song structure. According to this hypothesis, females preferentially choose mates who sing the same song dialect as their father, thus being assured of breeding with local males possessing genes genetically specialized for the local environmental conditions.

Payne's (1981) model of social adaptation proposes that song differences result from the social behaviour of interacting territorial males. In this model, song development is seen as intraspecific mimicry, with song mimics gaining a reproductive advantage over others in the ability to set up and maintain territories. The adaptive value of copying the song of other males is that by doing so a young male would give the deceptive impression of being an established male and be tolerated. In addition, by singing the song of a previous territory owner, a young male would deceive others into responding to him as if he were the former territory owner. Payne has used this hypothesis to account for the song variation patterns he found in the village indigobird (Vidua chalybeata).

Recently Payne (1981) discussed these three hypotheses and developed predictions from them about (a) the genetic structure of dialect populations, (b) the ecological structure of the habitats occupied by the birds, (c) the dispersal of birds between dialects, (d) the population size and area of dialects, (e) the stability of dialect boundaries and the songs of dialects, (f) the role of social interactions, (g) the behavioural function of song and (h) the behavioural development of song. By using these predictions, the

applicability of the three hypotheses to explain song variation in the brown creeper could be tested.

However, before I could begin to evaluate these predictions it was necessary to determine exactly how song varied in the brown creeper. To accomplish this, songs had to be carefully compared within and between populations (Wiens 1982) and in addition, data on the social organization and the process of song development gathered. Thus, the goals of this investigation were (1) to describe song variation within and between populations of brown creepers, (2) to investigate the song development process and relate it to the pattern of song variation and (3) to evaluate and discuss the alternative hypotheses for the origin and function of song dialects.

RESULTS

GENERAL DESCRIPTION OF SONG

The songs of male brown creepers are composed of loud sequences of slurs, whistles and harsh sounding notes ("Song" portion of Fig. 7.1). Songs are 1.9–4.5 s long and are composed of 5–14 notes. When patrolling their territories, males sing strings of songs which are sometimes but

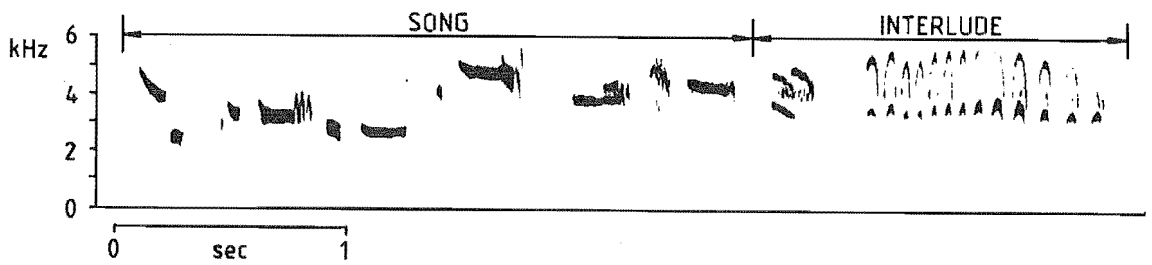

Fig. 7.1. Sonagram of the song and interlude of a male brown creeper recorded in Kowhai Bush.

not always interconnected by short interlude phrases ("Interlude" portion of Fig 7.1). Males that are vocally interacting with neighbours use single songs; (see pp. 67-68 for complete description of male song).

ONTOGENY OF MALE SONG

Based upon my observations and recordings, I have defined in chronological order three stages in the development of male song: subsong, plastic song and full song.

On the 28 June 1981 I observed and recorded MR-WR, a male who was known to be 228 days old, producing a low volume song-like vocalization (Fig. 7.2A), or subsong, which was composed of slurs that were variable in length and pitch and interspersed by harsh sounding notes. The pitch of each note was not held constant but exhibited irregular frequency modulation. MR-WR was heard singing subsong again on the 29 and 30 June and on the 1 July 1981. I also recorded three other young males of approximately the same age singing subsong at the same time of year.

By late September 1981 MR-WR sang a louder song, the notes of which showed greater structure than in the subsong (Fig. 7.2B). This stage, called plastic song, was not stereotyped, however, as notes were occasionally added to or subtracted from the sequence. Similar types of songs from two other males have been heard and recorded at about the same time of year.

MR-WR was first heard singing full song in mid-October 1981 (Fig. 7.2C). In contrast to both subsong and plastic song, full song was stereotyped and sung loudly.

To investigate whether young males learn their songs from their fathers or from neighbours with which they vocally interact, I examined the songs of males of known parentage. Only two males banded as nestlings were later found breeding and of these only one, MR-YW, set up

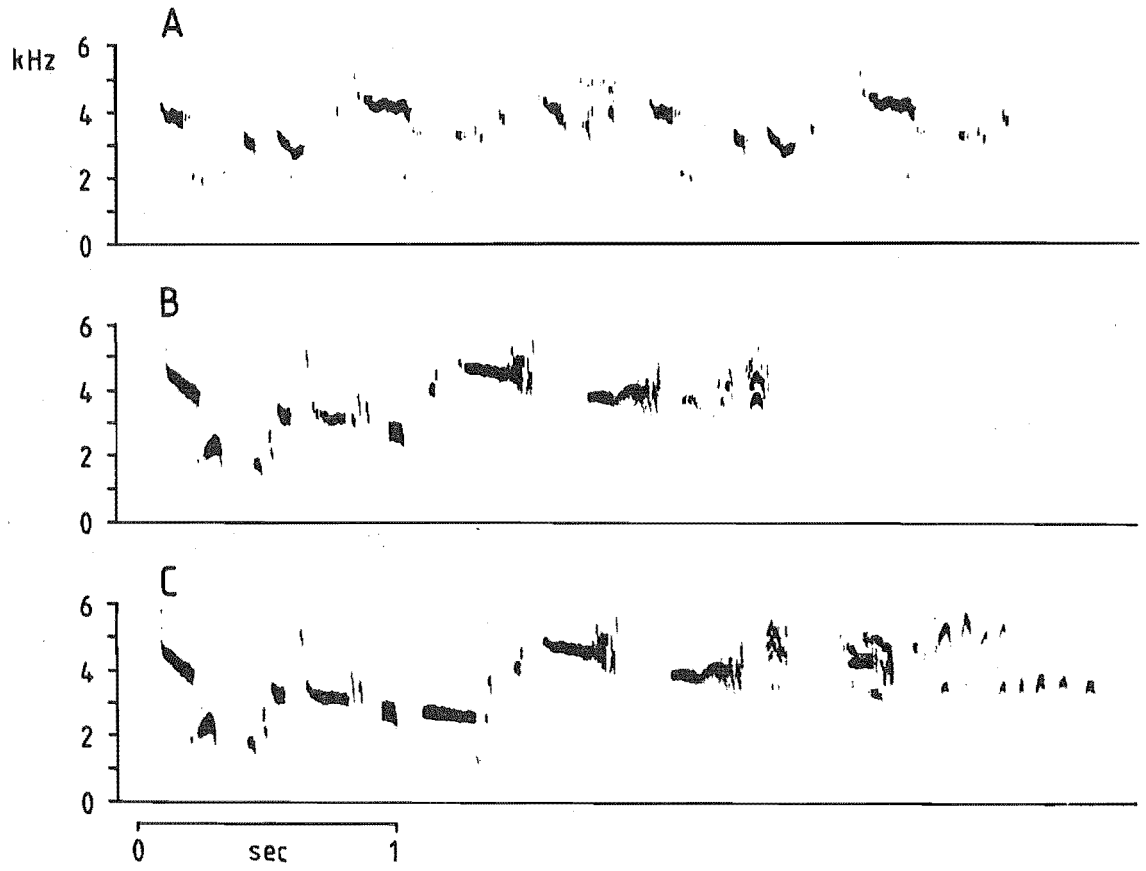

Fig. 7.2. Stages in the development of male song. A. subsong, B. plastic song, C. full song.

his territory away from his father's territory. MR-YW's song more closely resembled the song of his neighbour, M-R, than the song of his father (Fig. 7.3) suggesting that male brown creepers learn their songs from neighbours and not from fathers.

The songs of the two transferred males that had set up territories in the main study area were monitored to determine if adult males that have already begun to sing full song are capable of altering their song patterns when vocally interacting with new neighbours. The transfer took place on the 28 July 1982 and the two males were singing full song when captured.

Neither of the male's songs altered appreciably. MR-RB's songs remained the same (Fig. 7.4A and B) while MR-BB's song changed only slightly (Fig. 7.4C and D). Before the transfer, MR-BB's long and short songs (see description of Lake Rotorua dialect below) finished with a note that started as a whistle, increased rapidly in frequency and ended in another whistle (element "a" in Fig. 7.4B). This note remained unchanged in the long song (element "a" in Fig. 7.4D) but in the short song became a simple whistle (element "b" in Fig. 7.4D). MR-BB's neighbour, M-WW, with whom he frequently interacted, ended his song with a note of similar shape and pitch (element "b" in Fig. 7.4E). These results suggest that male brown creepers are limited in their capacity to alter their songs once full song has been developed.

VARIATION IN THE SONGS OF INDIVIDUAL BIRDS

The songs of two males, M-R and M-W, were analysed for individual variation in the 16 song characters I measured (see p. 15 for a list of song characters). Ten randomly selected songs were analysed for each male. The songs of M-R were recorded over a period of 27 months and those of M-W during 24 months.

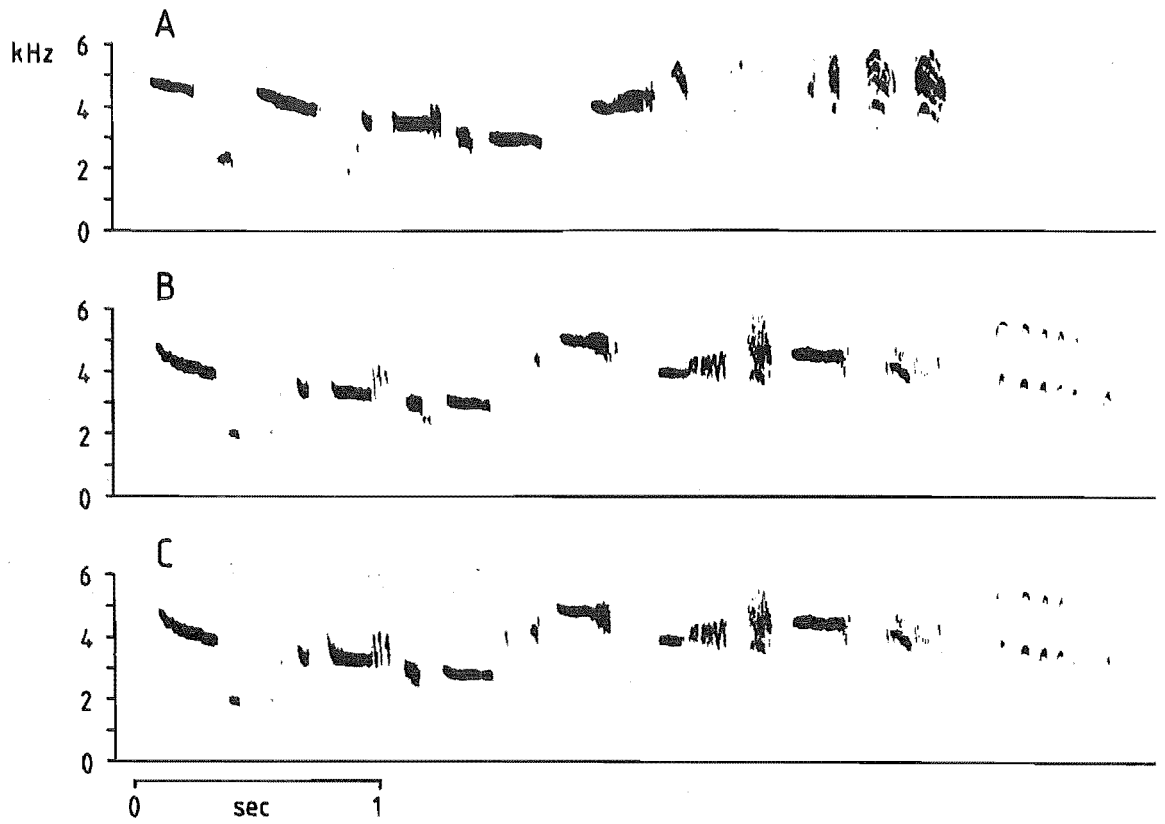

Fig. 7.3. Comparison of a male's song to his father's and neighbour's song. A. Song of male M-YG, B. song of M-YG's son (MG-W), C. song of MG-W's neighbour with whom he interacted (note that MG-W's song is more similar to his neighbour's song).

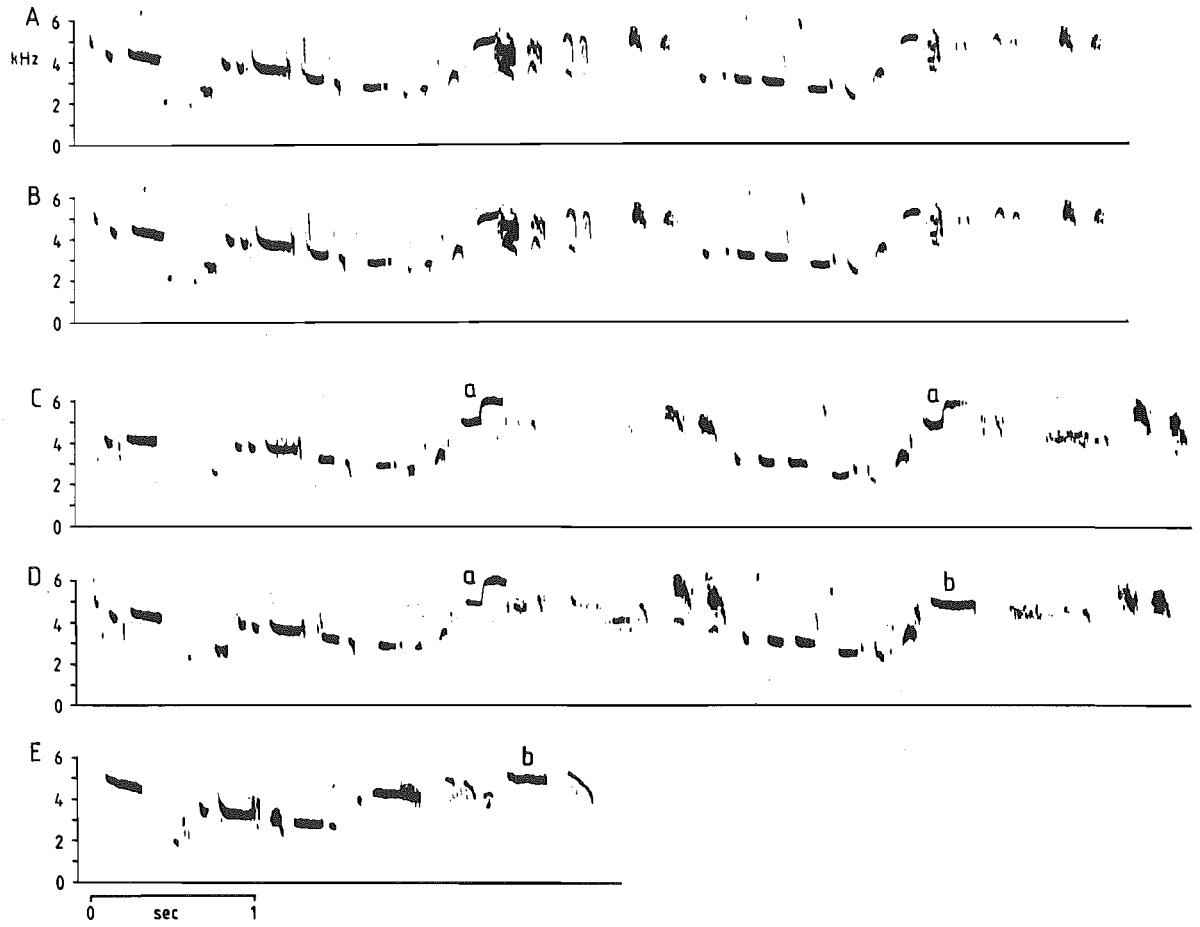

Fig. 7.4. Two Lake Rotorua males' songs before and after their transfer to Kowhai Bush and 1 Kowhai Bush male's song. A. MR-RB's song before transfer from Lake Rotorua. B. His song remained unchanged after transfer. C. MR-BB's song before transfer (note both song types ended with element "a"). D. MR-BB's song recorded in Kowhai Bush (note that element "b" has been introduced into the second song type). E. Song of MR-BB's neighbour, M-WW (note terminal element [b] of this song resembles "b" in MR-BB's song).

Coefficients of variation (C.V.) for the song characters were 0.63-8.33% for M-R and 0.32-10.0% for M-W (Table 7.1). As song characters with small mean values may be affected to a greater extent by measurement errors, those parameters such as SL, MXF and MNF probably give a more accurate indication of the amount of variation in the song of this species. Taking this into account, C.V. values were considerably lower and were 0.63-1.14% for M-R and 0.32-1.14% for M-W. These results strongly suggest that the songs of male brown creepers are highly stereotyped even over a two year period.

SONG VARIATION AMONG INDIVIDUAL BIRDS

C.V. values for the variation in the song characters among 10 randomly selected Kowhai Bush birds birds were 1.84-42.86%, while those characters with large means such as SL, NN, MXF, MNF and MFS had C.V. values of 1.84-16.33% (Table 7.2).

Variation among these birds was greater than that within male M-R or M-W for all song characters except VLN in male M-W and MNF in both males (Table 7.2; $F>4.00$; $P<0.05$). For both VLN and MNF the variation within a particular bird, however, was less than the population variation but not significantly so.

SONG SIMILARITIES BETWEEN NEIGHBOURING MALES

Generally, neighbouring males shared song patterns but retained individually distinctive interludes (Fig. 7.5). For example, the four males in group A of the main study area had contiguous territories and sang nearly identical songs. Their interludes were similar but the length of the terminal trills differed. In contrast, M-R (in group A) and M-WW (F) were not neighbours and had very different song patterns. Not all neighbouring males, however, shared similar song patterns. Males

Table 7.1 Descriptive statistics for 16 song characters of two male brown creepers.

Song Characters*	M-R				M-W			
	N	Mean	SD	C.V.	N	Mean	SD	C.V.
SL	10	2.64	0.003	0.11	10	3.14	0.01	0.32
NN	10	10	0.0	-	10	11	0.0	-
MLN	10	0.15	0.0	-	10	0.16	0.0	-
VLN	10	0.09	0.0	-	10	0.09	0.005	5.56
MIBN	10	0.12	0.005	4.17	10	0.13	0.005	3.85
VIBN	10	0.08	0.003	3.75	10	0.06	0.004	6.67
MXF	10	4.75	0.03	0.63	10	4.76	0.0	-
MNF	10	2.69	0.03	1.12	10	2.62	0.03	1.14
MFS	10	3.80	0.04	1.05	10	3.79	0.02	0.53
VFN	10	0.78	0.02	2.56	10	0.78	0.01	1.28
MCNL	10	0.15	0.005	3.33	10	0.16	0.0	-
VNLC	10	0.05	0.0	-	10	0.04	0.003	7.50
MCIBN	10	0.08	0.003	3.75	10	0.07	0.003	4.28
VCIBN	10	0.07	0.0	-	10	0.05	0.005	10.0
MCF	10	0.60	0.05	8.33	10	0.58	0.01	1.72
VFC	10	0.45	0.02	4.44	10	0.46	0.02	4.35

* see page 15 for explanation of song character abbreviations.

Table 7.2 Descriptive statistics for 16 song characters of 10 male brown creepers.

Song Characters*	Mean	SD	C.V.
SL	2.45	0.40	16.33
NN	9.20	1.14	12.39
MLN	0.15	0.02	13.33
VLN	0.09	0.008	8.89
MIBN	0.14	0.01	7.14
VIBN	0.08	0.02	25.00
MXF	4.74	0.23	4.85
MNF	2.71	0.05	1.84
MFS	3.69	0.12	3.25
VFN	0.75	0.07	9.33
MCNL	0.13	0.02	15.38
VNLC	0.06	0.02	33.33
MCIBN	0.08	0.02	25.00
VCIBN	0.07	0.03	42.86
MCF	0.53	0.10	18.87
VFC	0.48	0.10	20.83

* see page 15 for abbreviation of song characters.

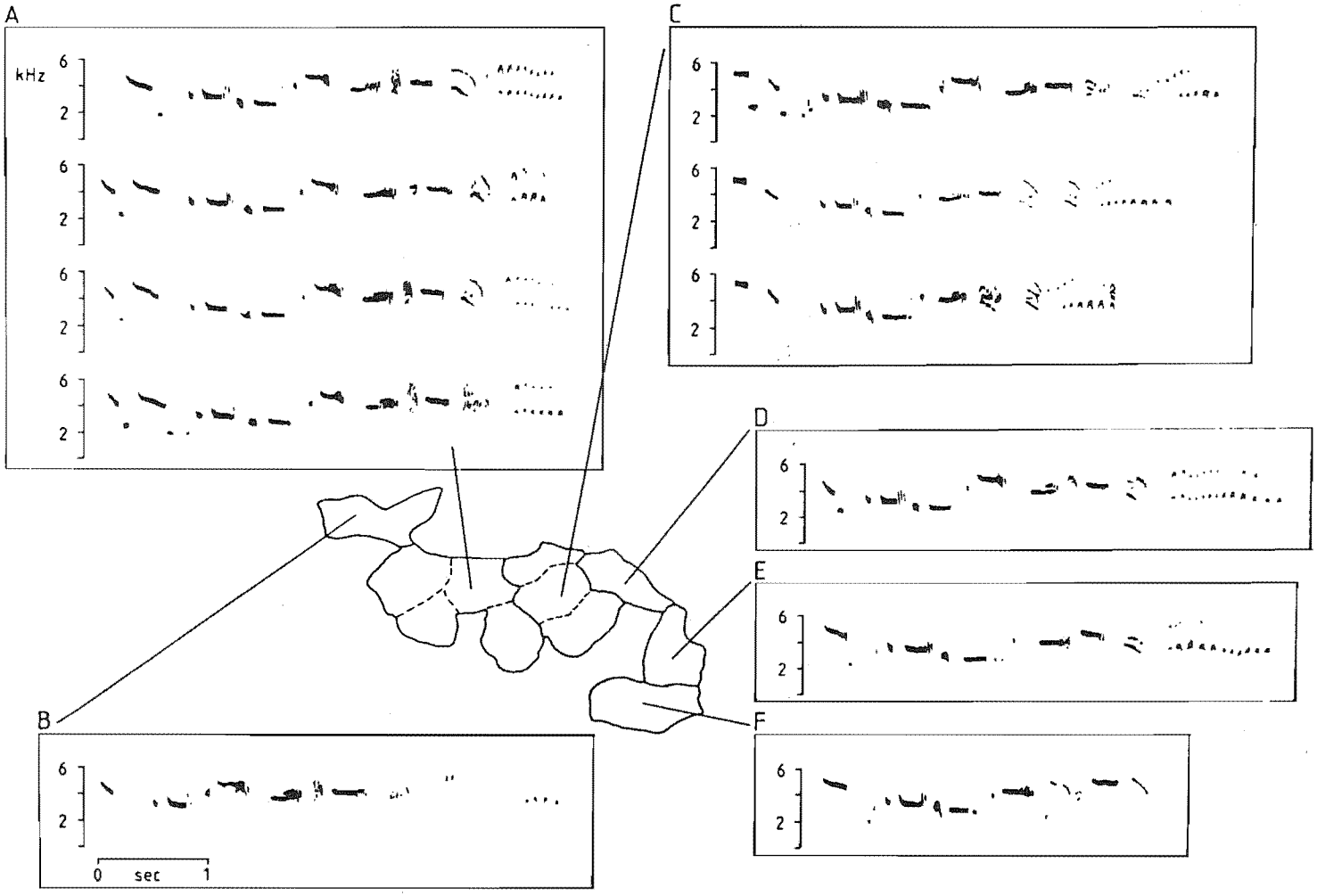

Fig. 7.5. Map showing the 1979-80 breeding territories within the main study area and the occupying males' songs and interludes. A. Group of neighbouring males sharing songs. Dotted lines show individual territorial boundaries. B. M-YR's song which was unlike his neighbours' songs. C. Neighbourhood of males singing similar songs. D to F. Males who sang a song not shared by neighbours.

MW-G (E) and M-WW (F) had adjoining territories but distinctly different songs. Those males that did share songs interacted frequently by singing in unison along their common territorial boundaries (Chapt. 10). Males that sang dissimilar songs either did not interact or did so infrequently.

DISTRIBUTION OF SONG PATTERNS IN KOWHAI BUSH

To determine if subdialects were formed, the 16 characters of songs from 49 males recorded in Kowhai Bush during the 1981-82 breeding season were subjected to principal component analysis (PCA). The correlation coefficients of the first four principal components show that those song characters with high eigenvalues in PC1 were MLN, MLIN, VINL, MFS, MCINL, VINL, and MCF (Table 7.3). PC2 was constructed of high eigenvalues for characters SL, MXF, MNF, VFN, and NN, PC3 for VLN and VCNL, and PC4 for VFC.

The first four principal components explain 72.4% of the variability (bottom line of Table 7.3). Morrison (1976) has suggested that the first four or five components should explain around 70-75% of the variability for the analysis to be meaningful. Thus this analysis explainsa significant amount of the total variability in the data.

A scatter diagram of the first versus the second principal components revealed that the songs of most males clustered together in the centre of the plot (Fig. 7.6). There were a few outlying songs such as those from males 20, 8 and 2. These results suggest that males in certain parts of Kowhai Bush tend not to sing songs which are markedly different from those sung in other parts of the forest. Evidence for the great similarity of songs within the population can also be seen from the the sonagrams of six Kowhai Bush males that were not neighbours (Fig. 7.8).

Table 7.3 Eigenvectors of 16 song characters in a principal component analysis.

Song characters*	Eigenvectors			
	PC1	PC2	PC3	PC4
SL	0.290	-0.627	0.527	-0.215
NN	-0.348	-0.719	0.134	-0.355
MLN	0.680	0.110	0.595	0.080
VLN	0.212	0.285	0.831	-0.012
MIBN	0.782	0.286	0.179	0.239
VIBN	0.768	0.278	-0.353	-0.000
MXF	0.561	-0.624	-0.057	-0.220
MNF	0.401	0.644	-0.225	-0.214
MFS	0.707	-0.166	-0.024	-0.314
VFN	0.376	-0.812	-0.107	0.168
MCNL	0.049	0.124	0.465	0.569
VNLC	0.044	0.276	0.694	-0.397
MCIBN	0.639	0.245	-0.404	-0.180
VCIBN	0.611	-0.005	-0.295	-0.136
MCF	0.799	-0.163	0.064	0.009
VFC	0.377	-0.447	-0.110	0.659
Component	4.598	3.029	2.527	1.424
Total cumulative variance	28.7%	47.7%	63.5%	72.4%

* see page 15 for abbreviation of song characters.

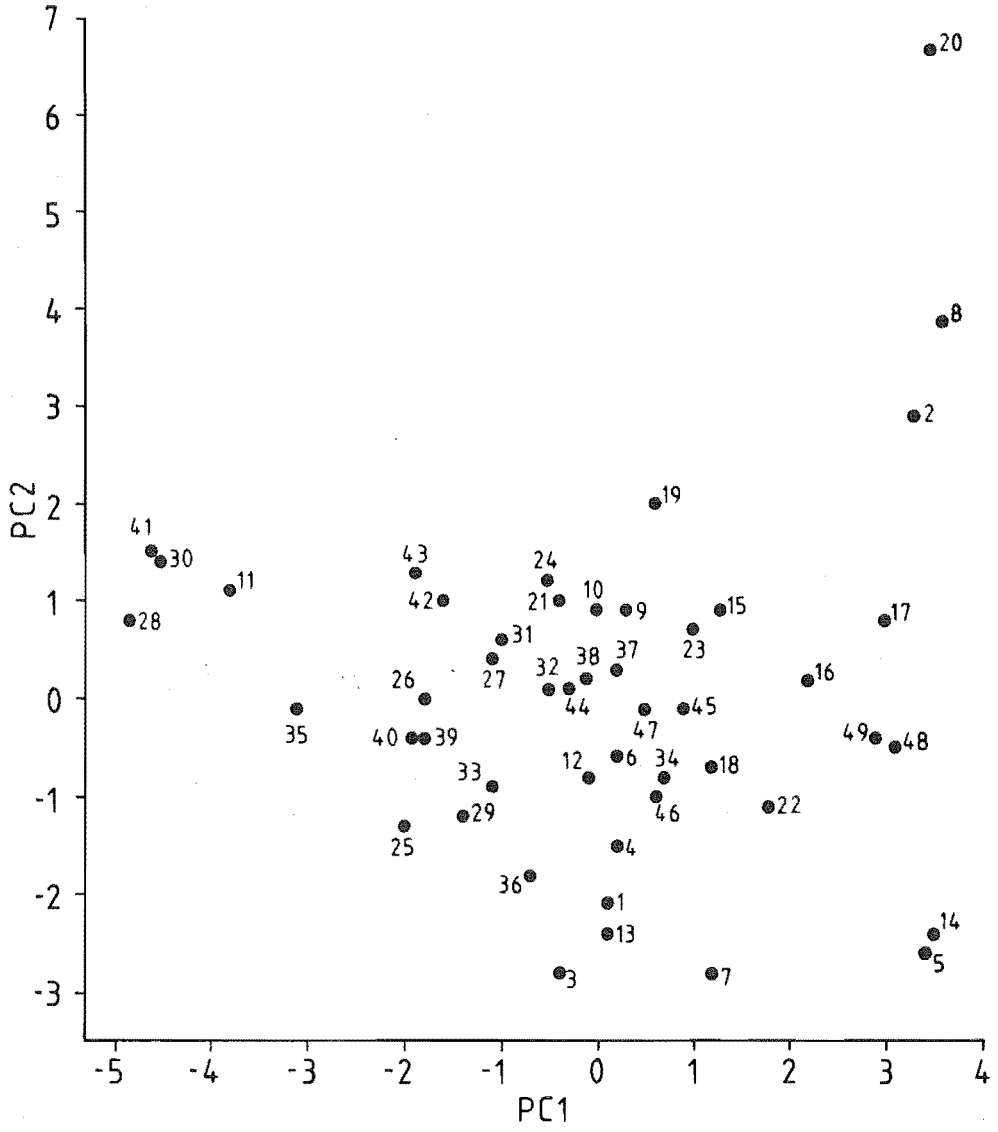

Fig. 7.6. Principal component ordination values of songs recorded from Kowhai Bush during the 1981-82 breeding season. Numbers correspond to individual birds shown in Fig. 7.7.

Although no distinct clusters emerged when PC1 versus PC2 were plotted, birds inhabiting the same region of the forest did sing similar songs and formed subdialects. The geographic location of males whose songs were analysed and plotted in Fig. 7.6 are indicated in Fig 7.7. For example, males 26, 27, 32, 42 and 43 inhabited the western edge of the forest between the floodway and Floodgate Creek and all clustered together in Fig 7.6. Their ordination values were between -0.5 and -2.0 in PC1 and 0.0 and 1.5 in PC2. Similarly, the songs of males who lived in the eastern edge of the forest (45, 46 and 47) had ordination values of 0.5 and 1.0 in PC1 and 0.0 and -1.0 in PC2.

SONG VARIATION BETWEEN FIVE KAIKOURA POPULATIONS

Descriptions of the Five Dialects

Kowhai Bush

Sonagrams of the songs and interludes of six of the 58 males recorded in Kowhai Bush are shown in Fig. 7.8. Of those males recorded, most began their songs with one or two slur notes. If two slurs were sung then they were unequal in length; the first being longer than the second. Songs sung by these males normally ended with 2-3 high pitched notes and the interlude phrase consisted of a rough sounding slur and a trill. The number of slurs and the number of elements making up the trill were highly variable between individuals.

West Bank

The songs of West Bank males often began with one short whistle followed normally by several notes which descended gradually in pitch (Fig 7.9). The song ended with a call-like note and one long high pitched whistle. Interludes consisted either of 2-3 rough sounding slurs or a slur followed by a trill.

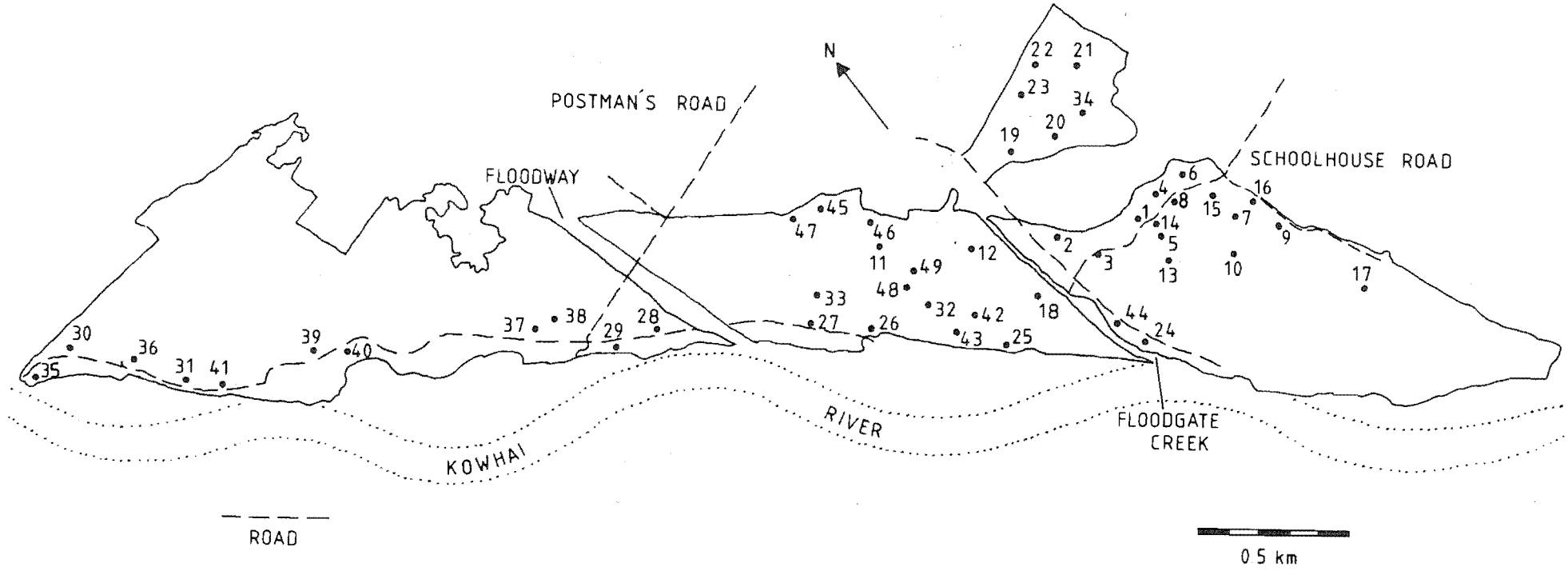

Fig. 7.7. Map of Kowhai Bush showing where males were recorded singing during the 1981-82 breeding season.

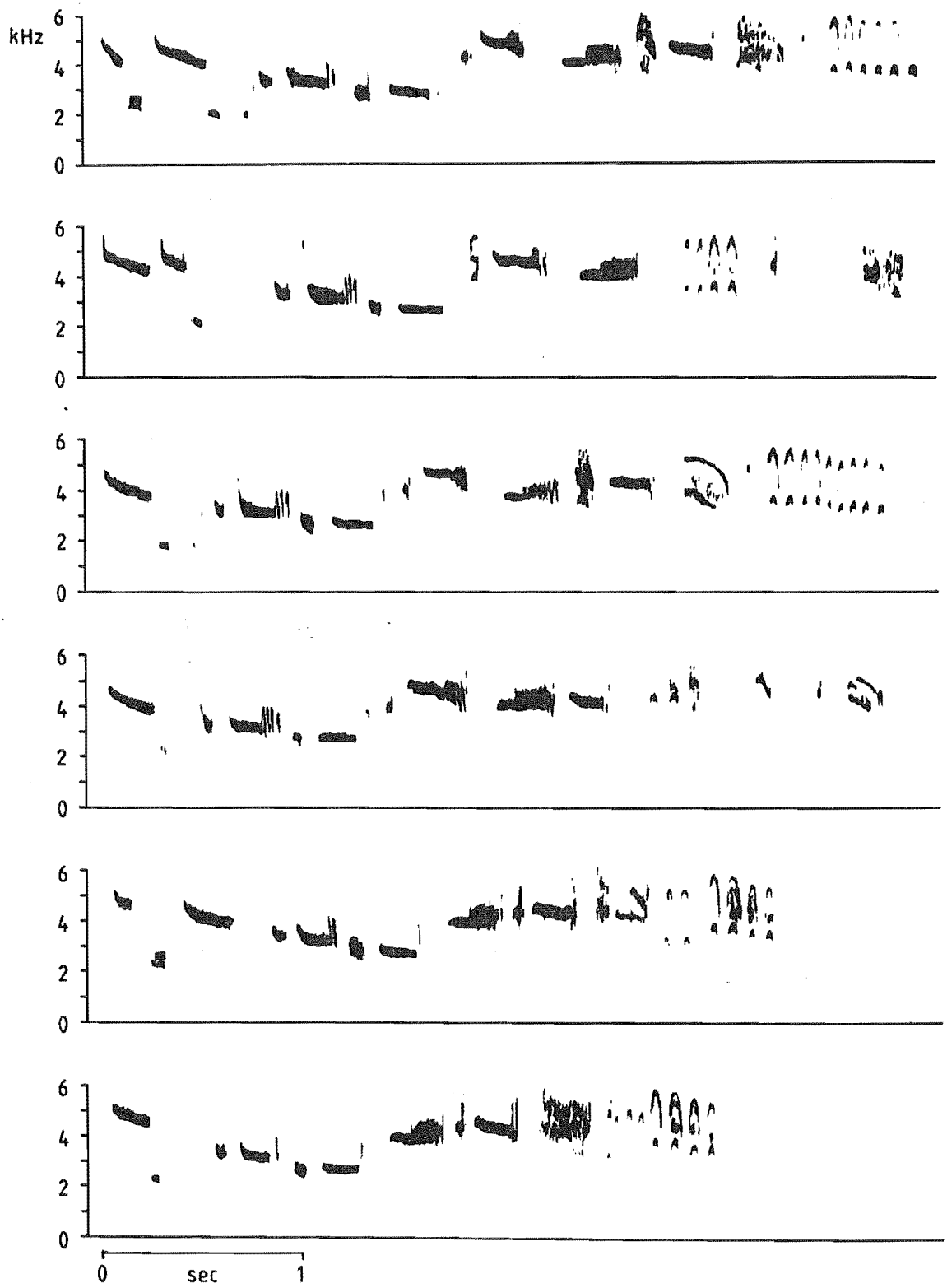

Fig. 7.8. Representative sonagrams of songs and interludes of the 58 males recorded in Kowhai Bush.

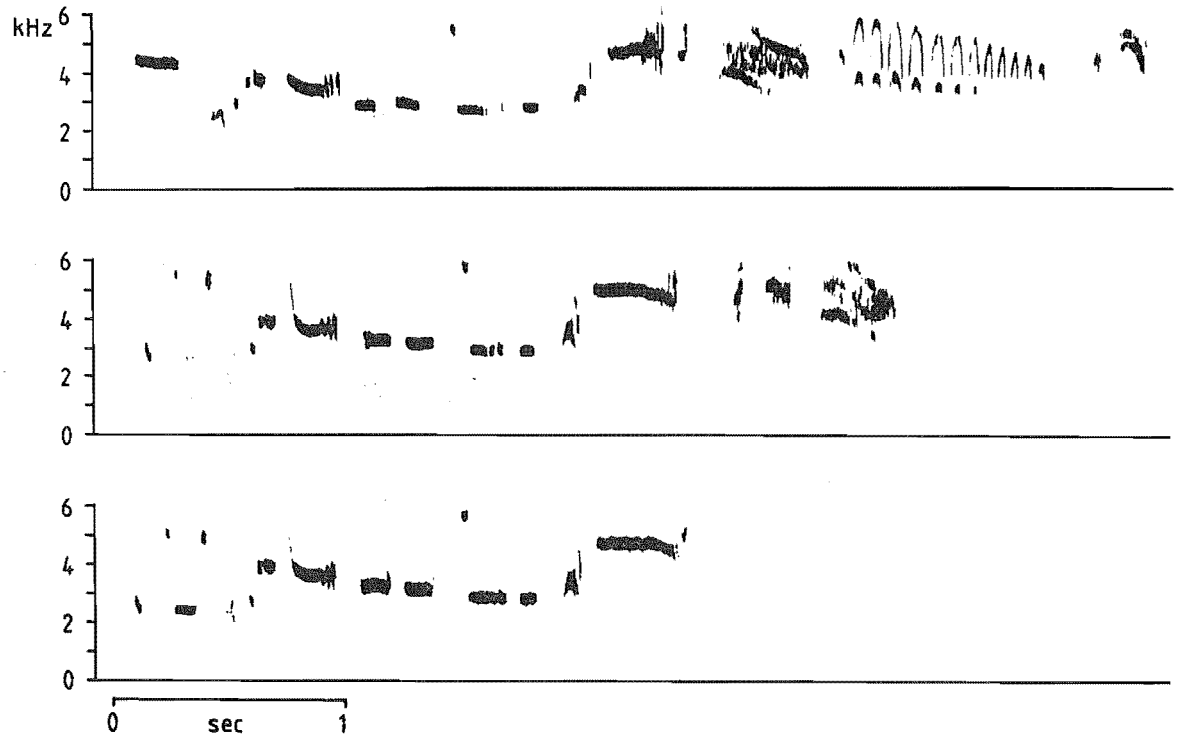

Fig. 7.9. Representative sonagrams of songs and interludes of the 14 males recorded on the West Bank of the Kowhai River.

Lake Rotorua

Males in the Lake Rotorua population differed from all others I recorded. They sang two song types; one about twice the length of the other. To illustrate this, sonagrams of songs of 4 representative males are presented in Figure 7.10. All the males recorded at Lake Rotorua began a singing bout by performing the longer of the two songs followed by an interlude and then the shorter song type which was normally repeated several times with an interlude between each short song.

The introductory notes of the long song consisted of two short notes and a whistle followed by 8-10 notes of variable lengths. The main song phrase usually ended with a chevron-shaped note and a whistle.

The short song type began with a series of six to eight notes and ended with a chevron note and a whistle, the last two notes being identical to those concluding the long song type. The interlude phrases sung in this population consisted normally of one to three rough sounding slurs or a rough slur followed by a trill.

Mount Fyffe

Representative sonagrams of the songs of 14 males from Mt. Fyffe show that the introductory notes of the songs consisted of 5-6 short notes (Fig. 7.11). Several whistles or slurs and a chevron-shaped note are then followed by 5-6 short notes and two whistles, of which the first is lower in pitch. The ends of these whistles were frequency modulated. The interlude, predominant in the population, was a trill and one or two rough sounding slurs or chevron-shaped notes.

Waimangarara River

Males in this dialect population began their songs with one or two long whistles which in some males tended to rise and fall in pitch near the end (Fig. 7.12). Following the whistles were five notes of variable length and one final high pitched whistle. The interlude varied

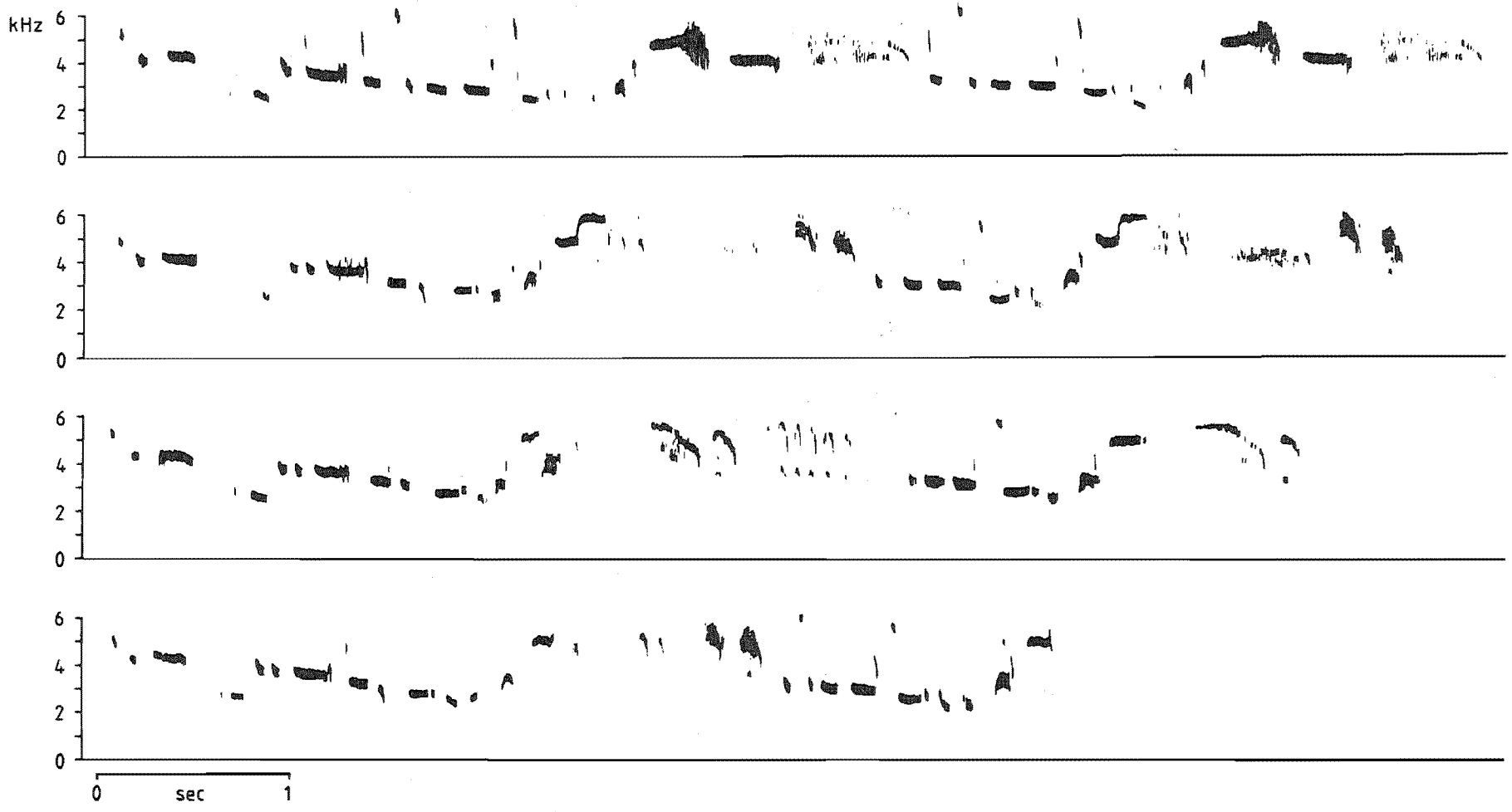

Fig. 7.10. Representative sonagrams of songs and interludes of the 29 males recorded at Lake Rotorua.

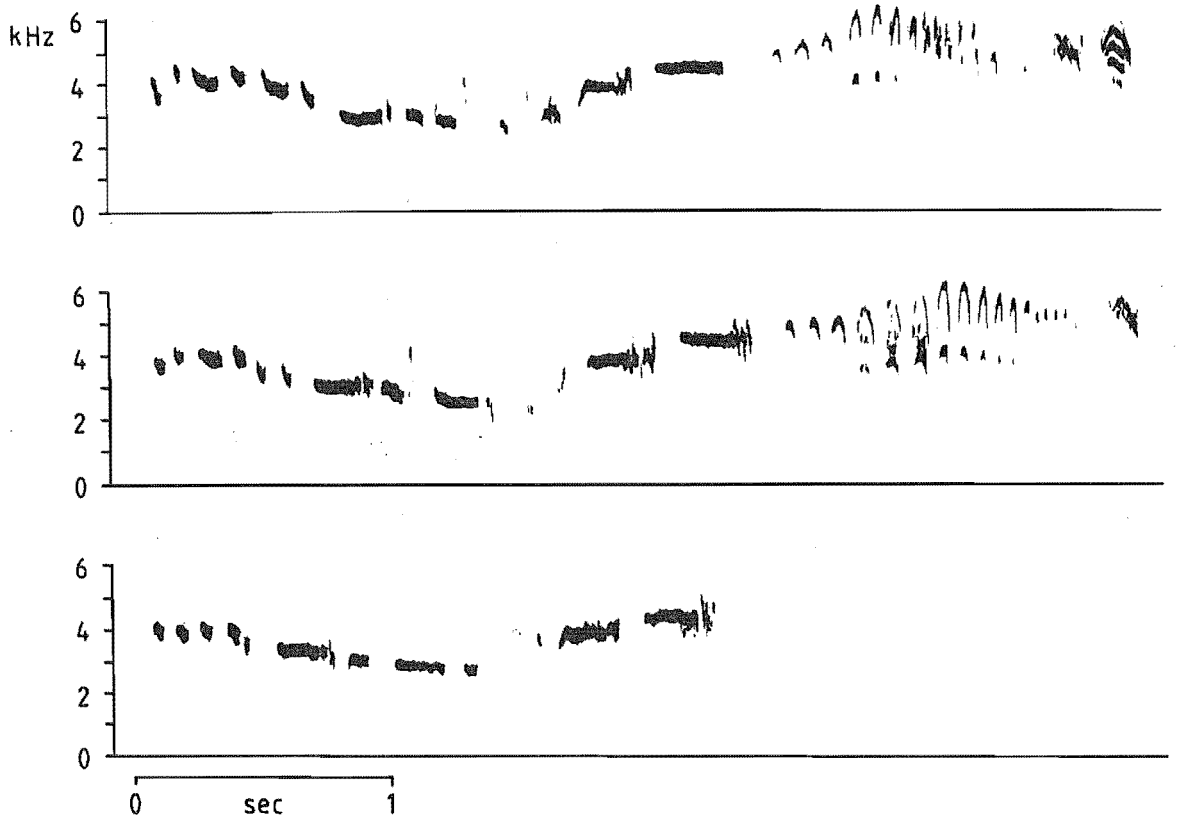

Fig. 7.11. Representative sonagrams of songs and interludes of the 14 males recorded on Mount Fyffe.

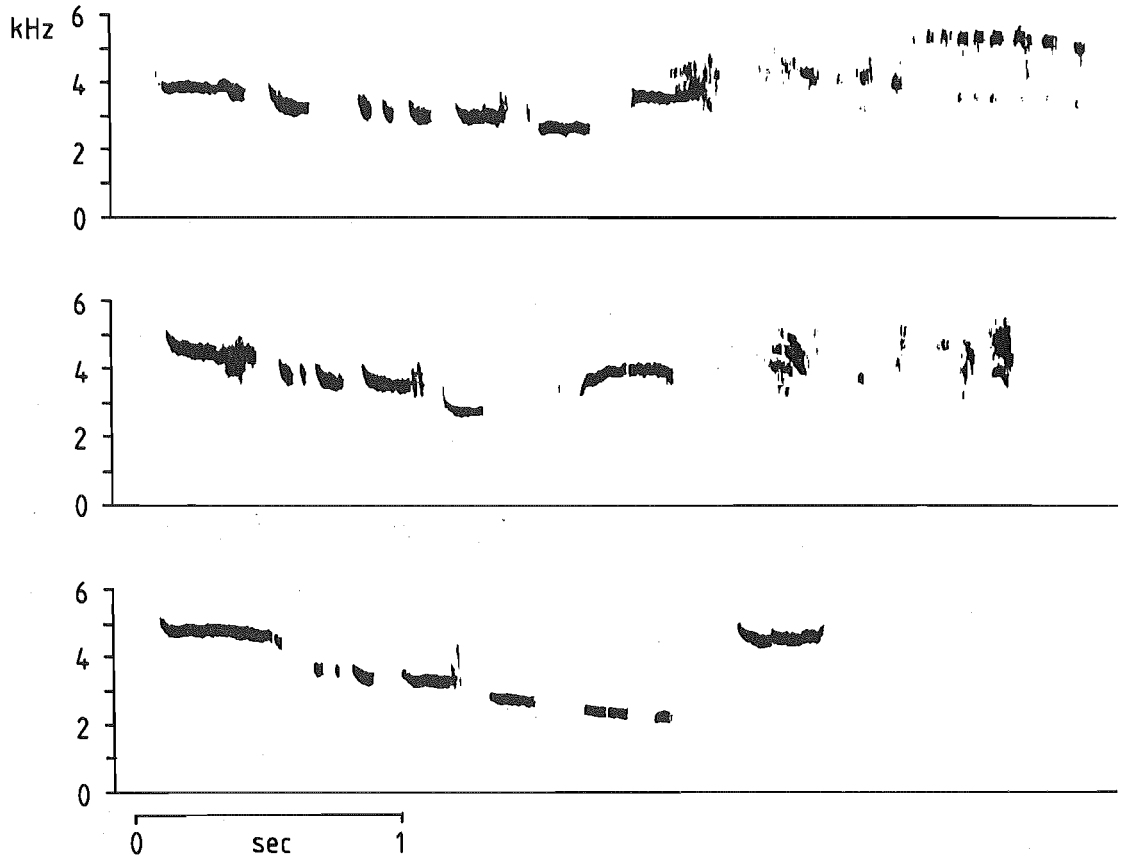

Fig. 7.12. Representative sonagrams of songs and interludes of the 10 males recorded at the Waimangarara River.

considerably in length from bird to bird and usually consisted of a rough sounding slur and a trill.

Quantitative Aspects of Song Variation

When descriptive statistics of the 16 song characters were computed for the 5 Kaikoura populations (Table 7.4) the populations were significantly different from one another in each of the song characters (see column 7 and 8 in Table 7.4 for results of one-way ANOVA).

To determine which pairs of populations were significantly different, I performed stepwise Student-Newman-Keuls (SNK) tests (Table 7.5). The Kowhai Bush and West Bank dialects were similar in 5 song characters, Kowhai Bush and Lake Rotorua in 2, Kowhai Bush and Mount Fyffe in 7 and Kowhai Bush and Waimangarara River in 3. West Bank and Lake Rotorua dialects resembled one another in 14 of the characters, West Bank and Mount Fyffe in 7 of the characters and West Bank and Waimangarara River dialects in 5. In 9 of the characters, the Lake Rotorua and Mount Fyffe dialects were similar while the Lake Rotorua and Waimangarara River dialects resembled each other in 7. Finally, Mount Fyffe and Waimangarara River dialects were similar in 8 out of the 16 song characters measured. In summary, the results of the SNK tests suggest that the songs sung by West Bank and Lake Rotorua birds were the most similar while the Kowhai Bush and Lake Rotorua dialects were the most dissimilar.

Song Characters Used in Song Discrimination

To objectively weigh the differences among the five Kaikoura song dialects and to determine which song characters best discriminate between these dialects, I subjected the data to a stepwise discriminant analysis. In discriminant analysis (Huberty 1975), functions are calculated which maximize the differences among the specified groups. The functions are linear models composed of weighted coefficients and standardized values

Table 7.4 Descriptive statistics (mean ± SD) of themes in five dialect populations in the Kaikoura area. KB=Kowhai Bush, WB=West Bank, LR=Lake Rotorua, MF=Mount Fyffe, WR=Waimangarara.

Song Characters*	Locations						
	KB (58)[a]	WB (14)	LR (29)	MF (14)	WR (10)	F	P<
SL	2.40 ± 0.35	2.39 ± 0.28	3.73 ± 0.28	2.45 ± 0.30	3.08 ± 0.40	65.96	0.001
NN	9.02 ± 1.11	13.0 ± 1.15	23.3 ± 1.70	11.62 ± 1.50	14.50 ± 1.00	344.21	0.001
MLN	0.14 ± 0.01	0.09 ± 0.01	0.08 ± 0.01	0.12 ± 0.01	0.16 ± 0.01	52.51	0.001
VLN	0.09 ± 0.01	0.07 ± 0.01	0.07 ± 0.01	0.08 ± 0.01	0.12 ± 0.01	28.54	0.001
MIBN	0.14 ± 0.02	0.10 ± 0.02	0.10 ± 0.02	0.11 ± 0.03	0.11 ± 0.02	16.38	0.001
VIBN	0.09 ± 0.01	0.07 ± 0.01	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01	9.13	0.001
MXF	4.68 ± 0.28	5.48 ± 0.35	5.37 ± 0.41	4.64 ± 0.42	4.61 ± 0.30	26.18	0.001
MNF	2.75 ± 0.10	2.55 ± 0.20	2.43 ± 0.17	2.32 ± 0.10	2.30 ± 0.14	34.01	0.001
MFS	3.69 ± 0.14	3.61 ± 0.10	3.50 ± 0.14	3.46 ± 0.10	3.46 ± 0.17	11.18	0.001
VFN	0.71 ± 0.10	0.93 ± 0.14	0.94 ± 0.14	0.71 ± 0.14	0.68 ± 0.10	20.24	0.001
MCNL	0.14 ± 0.02	0.08 ± 0.02	0.07 ± 0.02	0.08 ± 0.02	0.13 ± 0.02	73.22	0.001
VNLC	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01	0.11 ± 0.01	11.30	0.001
MCIBN	0.09 ± 0.02	0.08 ± 0.02	0.06 ± 0.02	0.04 ± 0.02	0.05 ± 0.02	12.77	0.001
VCIBN	0.08 ± 0.03	0.06 ± 0.02	0.06 ± 0.02	0.05 ± 0.03	0.04 ± 0.02	3.53	0.025
MCF	0.51 ± 0.10	0.98 ± 0.14	0.90 ± 0.14	0.42 ± 0.10	0.70 ± 0.10	39.62	0.001
VFC	0.44 ± 0.10	0.98 ± 0.10	0.93 ± 0.10	0.40 ± 0.17	0.64 ± 0.14	62.26	0.001

[a] = numbers of males recorded
* = see page 15 for abbreviation of song characters

Table 7.5 Patterns in the variation of song characters between the five Kaikoura populations. Localities and means joined by an underline are not significantly different ($p > 0.05$). WR=Waimangarara River, LR=Lake Rotorua, MF=Mount Fyffe, KB=Kowhai Bush, WB=West Bank.

Song character*	Locality				
SL	WR 3.82	LR 3.73	MF 2.45	KB 2.40	WB 2.39
NN	LR 23.3	WR 14.5	WB 13.0	MF 11.6	KB 9.0
MLN	WR 0.16	KB 0.14	MF 0.12	WB 0.09	LR 0.08
VLN	WR 0.12	KB 0.09	MF 0.08	WB 0.07	LR 0.07
MIBN	KB 0.14	MF 0.11	WR 0.11	WB 0.10	LR 0.10
VIBN	KB 0.09	WB 0.07	LR 0.06	MF 0.06	WR 0.06
MXF	WB 5.48	LR 5.37	KB 4.68	MF 4.64	WR 4.61
MNF	KB 2.75	WB 2.55	LR 2.43	MF 2.32	WR 2.30
MFS	KB 3.69	WB 3.61	LR 3.50	MF 3.46	WR 3.46
VFN	LR 0.94	WB 0.93	KB 0.71	MF 0.71	WR 0.68
MCNL	KB 0.14	WR 0.13	WB 0.08	MF 0.08	LR 0.07
VNLC	WR 0.11	KB 0.06	WB 0.06	LR 0.06	MF 0.06
MCIBN	KB 0.09	WB 0.08	LR 0.06	WR 0.05	MF 0.04
VCIBN	KB 0.08	WB 0.06	LR 0.06	MF 0.05	WR 0.04
MCF	WB 0.98	LR 0.90	WR 0.70	KB 0.51	MF 0.42
VFC	WB 0.98	LR 0.93	WR 0.64	KB 0.44	MF 0.40

* see page 15 for abbreviation of song characters.

of the variables used. In step-wise discriminant analysis only those variables that contribute a significant amount to the functions are included. The total number of functions is either equal to one less than the number of groups or to the number of variables, whichever is the smaller.

I found that 9 of the 16 song characters contained enough information to contribute to the discrimination of the five populations (Table 7.6). These nine characters were SL, NN, MLN, VLN, MIBN, MNF, MFS, MCNL and VFC and separated 97.6% of the 125 songs analysed into the correct song dialects.

When function 1 versus function 2 was plotted a complete separation of the five populations occurred (Fig. 7.13). Each population is represented by a polygon that encloses all data points for that population. Function 1 divided West Bank and Waimangarara River songs from Kowhai Bush and Mount Fyffe songs. In addition, the first function separated the Lake Rotorua dialect songs from the other four. Separation on the first axis (function 1) was based mainly on three song characters: number of notes in the songs (NN), variation in the mean change in note frequency (VFC) and the minimum frequency in the songs (MNF) (Table 7.6). Function 2 divided West Bank songs from Waimangarara River songs and the Kowhai Bush dialect from that of Mount Fyffe. The separation in the second axis (function 2) was due primarily to high scores in two additional song characters: song length (SL) and variation in mean note length (VLN) (Table 7.6).

SONG VARIATION BETWEEN THREE STEWART ISLAND POPULATIONS

Descriptions of the Dialects

Ulva Island

The songs sung by Ulva Island males began with a short whistle

Table 7.6 Standardized canonical coefficients of discriminating song characters of brown creepers in the Kaikoura Area.

Song characters*	Functions			
	I	II	III	IV
SL	0.211	-0.842	-0.428	0.459
NN	-1.458	0.794	-0.077	-0.635
MLN	0.137	0.245	-0.432	-0.683
VLN	-0.404	-0.789	-0.142	0.965
MIBN	-0.516	0.499	0.378	-0.393
MNF	-1.018	0.638	-0.297	0.594
MFS	0.605	0.085	0.252	0.114
MCNL	0.162	0.499	0.435	-0.025
VFC	-0.885	-0.042	-0.233	1.133
Accumulated proportion of total dispersion	86.1%	92.3%	96.4%	100.0%

* see page 15 for abbreviation of song characters.

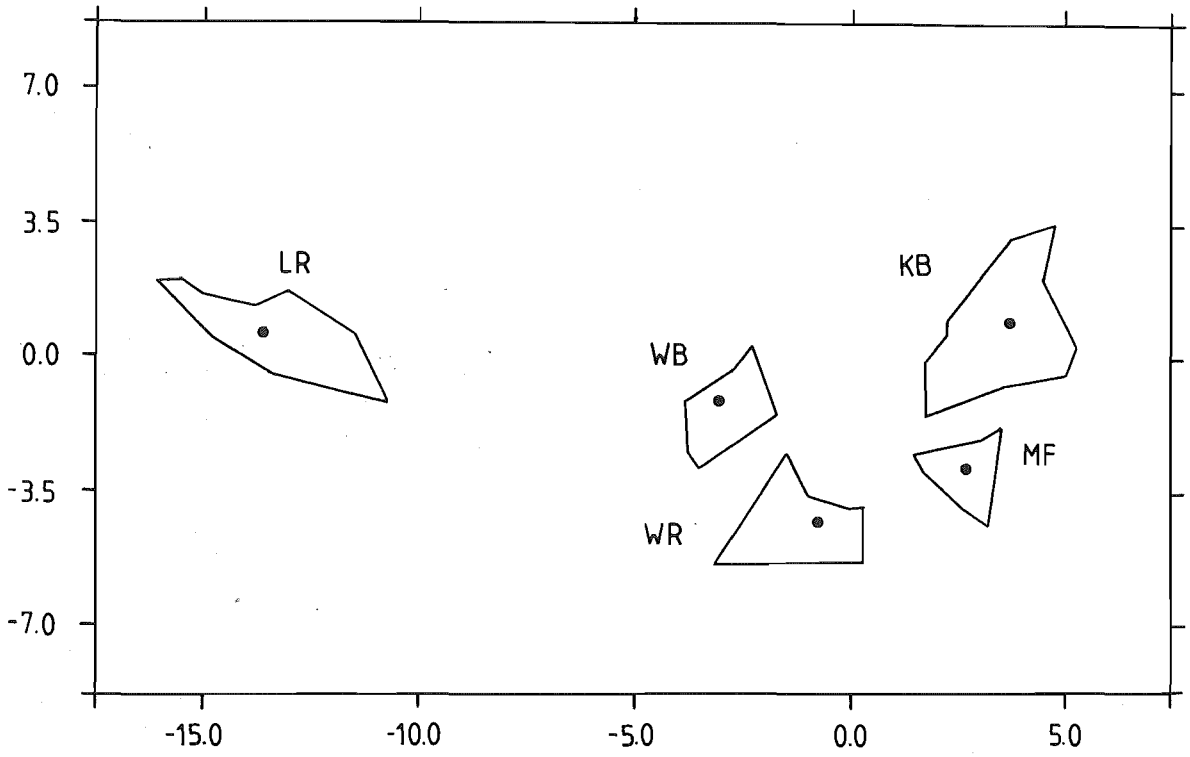

Fig. 7.13. Discriminant function analysis of songs from the five Kaikoura populations, showing factor 1 (x-axis) and 2 (y-axis). Polygons enclose the largest area among the points of individual songs.

that ended with 2-3 peaks followed by 7-8 notes that increased slightly in pitch (see representative sonagrams; Fig. 7.14). These notes were slurs, whistles and rough sounding slurs. The songs concluded with 1-3 whistle notes which were of similar pitch to the introductory one. None of the males recorded ever sang an interlude between consecutive songs.

Freshwater Flat

Sonagrams from the Freshwater Flat population show that the songs began with one or two short notes that were followed by four whistles that descended in pitch (Fig. 7.15). These songs finished with three short notes and a long whistle. No interludes were recorded from these males.

Mason Bay Track

Two sonagrams of the songs sung by males in this population are presented in Figure 7.16. The brown creeper males along the Mason Bay track started their songs with two short notes and a long whistle. These introductory notes were followed by 3-4 whistles that descended in pitch and one chevron note followed by a long high-pitched whistle.

Quantitative Aspects of Song Variation

Descriptive statistics for the Stewart Island dialects were calculated (Table 7.7). When one-way ANOVAs were completed for each character, only song length was not significantly different between the populations.

For those characters in which the 3 populations were different, a SNK test determined which pairs of populations were different (Table 7.8). All three populations appeared to be equally dissimilar when the number of variables which were significantly different were examined. The Ulva Island and Freshwater Flat dialects were similar in only four of the 16 song characters and Ulva Island and Mason Bay dialects in three.

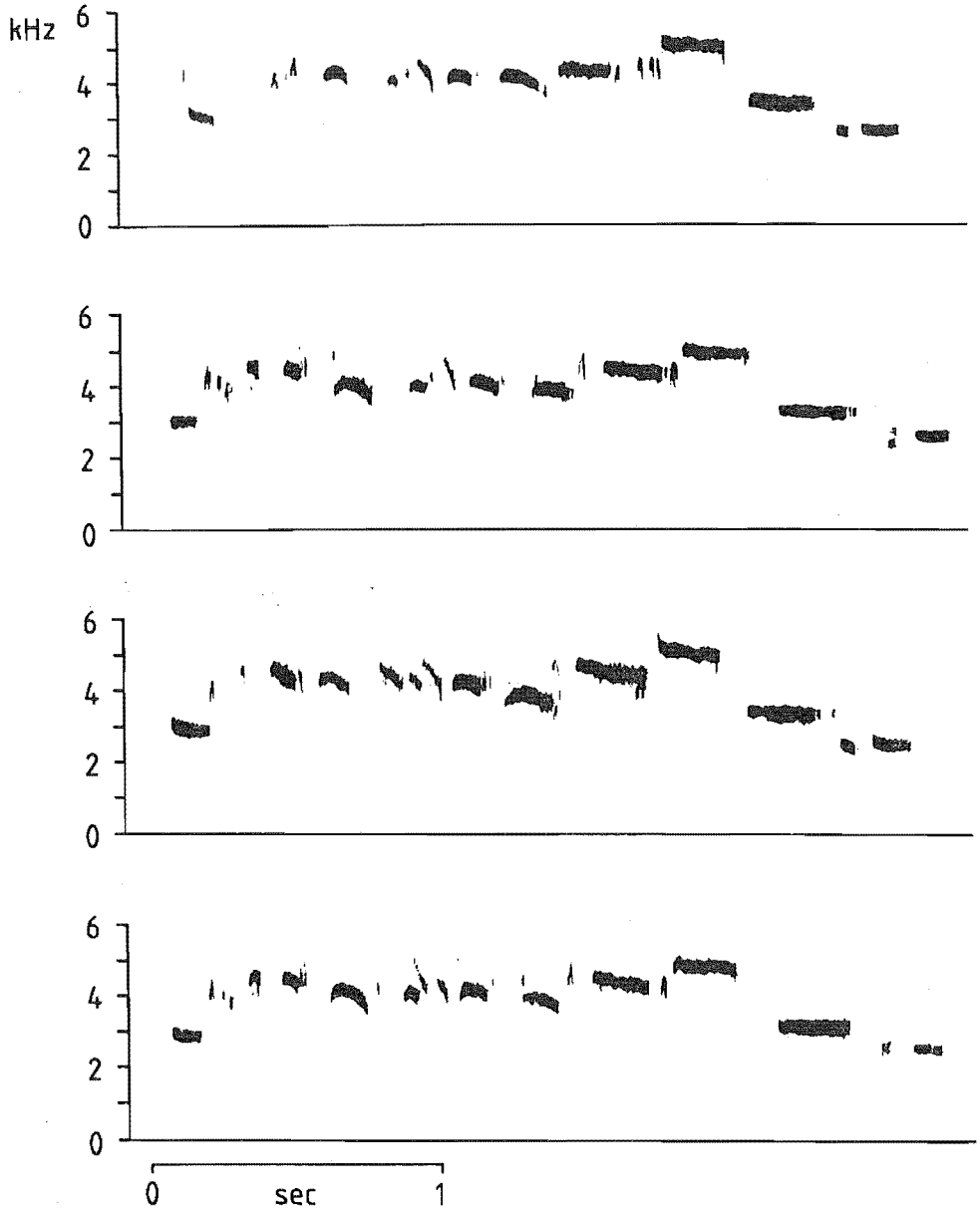

Fig. 7.14. Representative sonagrams of songs and interludes of the 22 males recorded on Ulva Island.

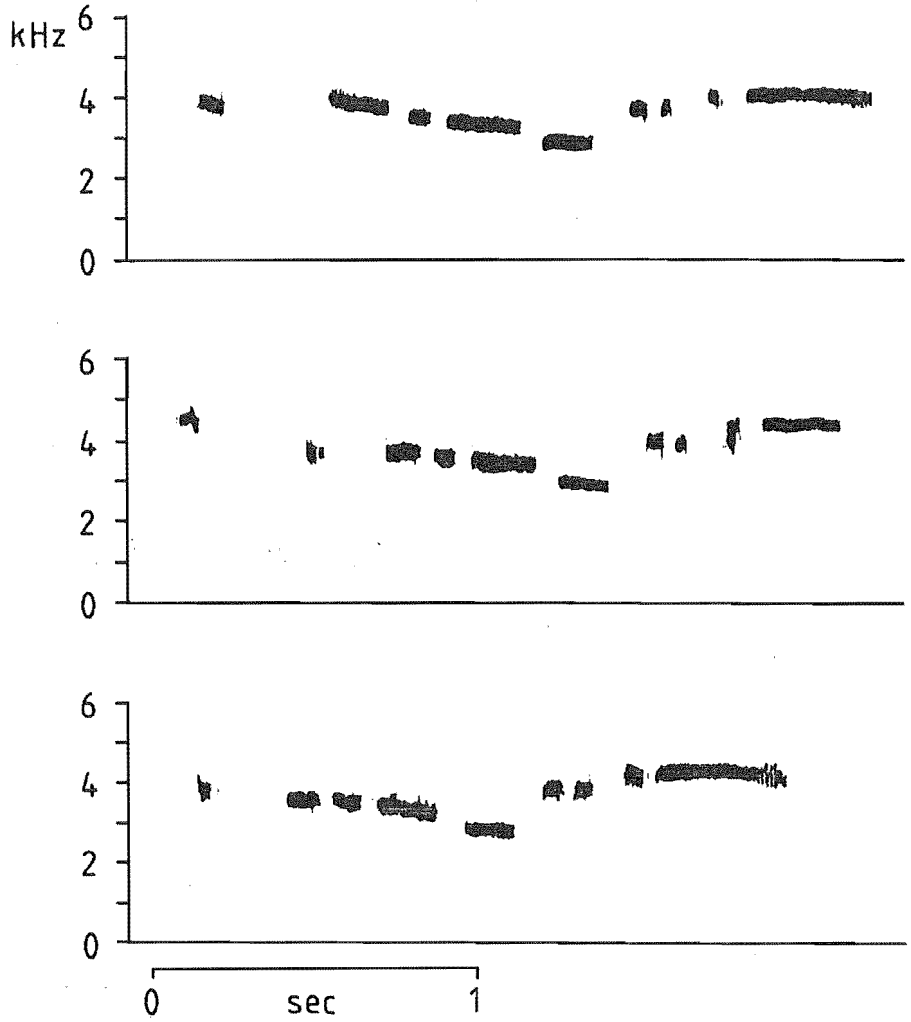

Fig. 7.15. Representative sonagrams of songs and interludes of the 8 males recorded at Freshwater Flat.

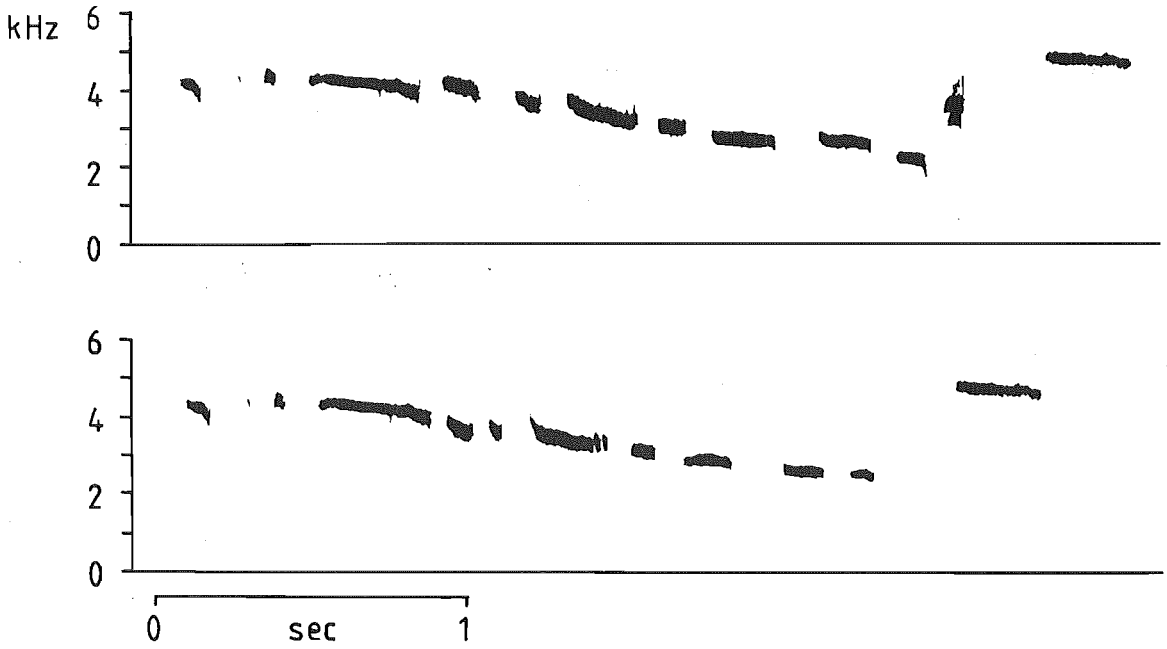

Fig. 7.16. Representative sonagrams of songs and interludes of the 5 males recorded on the Mason Bay Track.

Table 7.7 Descriptive statistics (mean ± SD) of themes in 3 dialect populations on Stewart Island. UI=Ulva Island, FF=Freshwater Flat, and MB=Mason Bay Track.

Characters	Locations				
	UI (22)	FF (8)	MB (5)	F	P<
SL	2.81 ± 0.26	2.43 ± 0.19	2.82 ± 0.12	2.24	NS
NN	13.3 ± 0.78	13.0 ± 0.60	11.0 ± 0.51	5.37	0.025
MLN	0.13 ± 0.01	0.08 ± 0.01	0.17 ± 0.02	46.16	0.001
VLN	0.07 ± 0.01	0.08 ± 0.02	0.14 ± 0.01	54.69	0.001
MIBN	0.08 ± 0.01	0.11 ± 0.01	0.09 ± 0.02	7.16	0.005
VIBN	0.04 ± 0.01	0.12 ± 0.01	0.02 ± 0.01	95.71	0.001
MXF	5.09 ± 0.15	4.36 ± 0.20	4.05 ± 0.11	60.10	0.001
MNF	2.51 ± 0.10	2.78 ± 0.12	2.57 ± 0.10	16.71	0.001
MFS	3.87 ± 0.10	3.44 ± 0.13	3.32 ± 0.09	102.29	0.001
VFN	0.79 ± 0.06	0.60 ± 0.05	0.65 ± 0.03	16.16	0.001
MCNL	0.08 ± 0.02	0.05 ± 0.02	0.16 ± 0.01	27.94	0.001
VNLC	0.05 ± 0.01	0.08 ± 0.03	0.13 ± 0.02	51.12	0.001
MCIBN	0.04 ± 0.01	0.10 ± 0.01	0.02 ± 0.01	37.31	0.001
VCIBN	0.03 ± 0.01	0.14 ± 0.02	0.02 ± 0.01	101.64	0.001
MCF	0.49 ± 0.05	0.28 ± 0.04	0.40 ± 0.07	19.47	0.001
VFC	0.50 ± 0.06	0.38 ± 0.02	0.38 ± 0.02	10.41	0.001

Table 7.8 Patterns in the variation of song characters between the three Stewart Island populations. Localities and means joined by an underline are not significantly different ($p > 0.05$). MB=Mason Bay Track, UI=Ulva Island, and FF=Freshwater Flat.

Song character*	Locality		
SL	MB 2.82	UI 2.81	FF 2.43
NN	UI 13.3	FF 13.0	MB 11.0
MLN	MB 0.17	UI 0.13	FF 0.08
VLN	MB 0.14	FF 0.08	UI 0.07
MIBN	FF 0.11	MB 0.09	UI 0.08
VIBN	FF 0.12	UI 0.04	MB 0.02
MXF	UI 5.09	FF 4.36	MB 4.05
MNF	FF 2.78	MB 2.57	UI 2.51
MFS	UI 3.87	FF 3.44	MB 3.32
VFN	UI 0.79	MB 0.65	FF 0.60
MCNL	MB 0.16	UI 0.08	FF 0.05
VNLC	MB 0.13	FF 0.08	UI 0.05
MCIBN	FF 0.10	UI 0.04	MB 0.02
VCIBN	FF 0.14	UI 0.03	MB 0.02
MCF	UI 0.49	MB 0.40	FF 0.28
VFC	UI 0.52	FF 0.38	MB 0.38

* See page 15 for abbreviation of song characters

In addition, the Freshwater Flat and Mason Bay dialects were similar in five of the song characters.

DISCUSSION

SONG DEVELOPMENT

Male brown creepers learn their song in three stages; subsong, plastic song, and full song. Similar steps, which Marler and Peters (1982) have concluded may be universal in the oscines, have been described for a number of song bird species (Nottebohm 1970). The brown creeper's subsong and plastic song were highly variable and lacked stereotyped patterns. One reason for this may be that subsong allows young males to develop the skills of singing, especially the precise coordination of the two sides of the syrinx (Nottebohm 1972). Once young males learned their song, it was stable and they appeared to have little ability to change it. Although neither of the transferred males modified his song significantly, a larger sample size may have produced different results. Thus, the possibility that my observations were the result of sampling error cannot be completely ruled out.

On the other hand, whether or not a bird changes his song may depend on the diversity of songs it hears when young (J. Craig, pers. comm.). Young males who flock and wander widely during the winter months may have the opportunity to hear several song dialects before their own song has been learned. Dialect populations of brown creepers, however, are often isolated physically from one another by uninhabitable areas such as farmlands or riverbeds. Thus, the two transferred birds may not have heard other dialects before they developed their song and were not able to learn them later. Before song development, young saddlebacks (Philesturnus carunculatus) and white-crowned sparrows (Zonotrichia

leucophrys nuttali) are exposed to several song dialects and are capable of modifying their songs after moving to a new territory (Jenkins 1977, Baptista 1975, Baptista and Petrinovich 1984).

A third possibility for the inability of brown creepers to vary their songs may be that they do not possess the behavioural plasticity of saddlebacks and white-crowned sparrows. Brown creepers are sedentary once established on a territory and may not require the neurological flexibility needed to modify songs. Saddlebacks, in contrast, frequently change their territories from one breeding season to the next and need to vary song patterns in order to interact effectively with new neighbours.

Social interactions also play an important role in brown creeper song development. When setting up his territory a young male learned the songs of the neighbours with whom he interacted and not that of his father. In addition, within a population, males that interacted socially shared songs while those that did not had dissimilar songs. This indicates that the songs heard early in life have only a limited influence in dictating the eventual song pattern used by a male. The importance of song learning through social interactions is well known in some other species (Thielcke 1970, Kroodsma 1974, Verner 1975, Payne and Payne 1977, Jenkins 1977, Todt et al. 1979).

SONG VARIATION

The songs of male brown creepers varied little between years and thus exhibited a high degree of song stability. This is of interest because it shows that males, even when confronted by different neighbours, retain their song patterns. In contrast, Jenkins (1977) found that resident male saddlebacks sometimes modified their songs to match songs of newly arrived neighbours. Thus the songs of saddlebacks are less stable over the life of a bird than they are in the brown

creeper.

Within populations of brown creepers, songs tended to be relatively uniform. However, upon closer examination, populations also exhibited a mosaic pattern of subdialects, with neighbouring males that vocally interacted singing similar or identical song patterns. Baptista (1975) also found subdialects in populations of white-crowned sparrows.

The results of comparisons of songs from different locations clearly demonstrates the existence of song dialects in the brown creeper. Dialects may have resulted from geographic isolation, since each population inhabits a patch of forest isolated from others by farmland. The song dialect within each of these populations might have gradually developed through the accumulation of errors in song learning. Baptista (1975) and Lemon (1975) from their work on other species, have also suggested that song dialects may have evolved as a result of isolation.

EVALUATION OF HYPOTHESES EXPLAINING DIALECT ORIGIN AND FUNCTION

The data I obtained on song development and song variation in the brown creeper as well as information gathered previously on the species' social organization and population structure (Chapts. 4 and 5) were used to test the predictions of the three hypotheses discussed by Payne (1981) (summary; Table 7.9). In some cases the predictions are mutually exclusive allowing one to determine which hypothesis best explains the data. Where applicable, predictions were evaluated for both dialects and subdialects

(A) Genetic Structure of Populations

The only model that makes a prediction in this area is the racial one. This assumes that dialect populations are genetically distinct. As I did not measure genetic differences between the populations studied this prediction cannot be directly evaluated. However, song differences

Table 7.9 Summary of evaluations of Payne's (1981) predictions from three hypotheses based on observations of brown creeper song variation at the subdialect(A) and dialect(B) levels. +=data support prediction, -=data reject prediction, ?=no prediction by Payne.

		Hypotheses		
		Racial Specialization	Historical	Social Adaptation
Genetic structure	B	-	?	?
Ecological structure	B	-	?	?
Dispersal	B	+	+	-
Population size and area	A	-	?	+
	B	+	+	-
Stability of boundaries and songs	A	-	+	+
	B	-	-	+
Social interactions	B	?	?	+
Function of song	B	-	?	+
Song development	B	-	?	+

between the Kowhai Bush and Mount Fyffe populations did exist and dispersal between them has been noted. On three separate occasions during the winters of 1980 and 1981 I observed flocks of brown creepers moving from Kowhai Bush into the forest on Mount Fyffe. This suggests that genetic differences between the two populations do not exist or are only slight even though the songs are dissimilar. Thus, the prediction of the racial hypothesis has to be rejected.

(B) Ecological Structure of Habitats

The prediction based on the racial model suggests that dialect boundaries will correspond to changes in habitat types. Neither of the other two hypotheses make assumptions of this kind. All five Kaikoura dialect populations which were studied inhabited similar types of forests. This observation does not support the prediction of this model. On Stewart Island, both the populations at Freshwater Flat and Mason Bay Track inhabited low growing manuka forests but the Ulva Island birds lived in tall mature groves. These points might support the prediction of the racial model, however, I feel it is more likely that the unique song pattern on Ulva is due to the island's isolation. The island is separated from the rest of Stewart Island by 5 km of open water.

(C) Dispersal Between Dialects Areas

The hypothesis of social adaptation assumes that there will be substantial dispersal across dialect boundaries whereas the racial model predicts little movement between populations and the historical one, limited dispersal. Brown creepers may move between some dialect populations (see above), but between many this could be limited. I suggest that farmland and riverbeds, which are devoid of forest vegetation, probably act as barriers which control diffusion of birds. This conclusion of low or limited dispersal supports either the racial or historical hypotheses.

(D) Population Size and Area of Dialects

The historical and racial hypotheses predict that both the number of males singing a dialect and the size of the dialect area will be highly variable. The social adaptation hypothesis, in contrast, assumes low variability in either of these parameters. I found that the number of male brown creepers singing one dialect and the area that the dialect group occupied was highly variable. Over 100 males spread over an area of 240 ha, sang the Kowhai Bush dialect; in contrast, 20 males used the Mount Fyffe theme which covered ca. 20 ha. These results support the historical or racial hypotheses. However, if we examine the number of males using specific subdialects, the picture is different. Variation is low for the number of males composing subdialects groups. Subdialect groups were composed of 2-5 males and were physically limited by constraints on the number of males that could interact socially. Therefore my observations of subdialects uphold the social adaptation model.

(E) Stability of Dialect Boundaries and Songs

Both the historical and racial hypotheses predict that the boundaries of song dialects and the songs sung by birds within dialects will be stable from year to year. In contrast, the social model suggests that both of these factors will be highly unstable. Between 1979 and 1984 the boundaries and songs of the Kowhai Bush and Lake Rotorua dialects did not change appreciably. This was also true of the Mount Fyffe dialect. These limited data, thus support the prediction of both the historical and racial specialization models and reject the social adaptation hypothesis.

However, the boundaries and songs of subdialects were very unstable. For instance, within the main study area there was a subdialect group composed of three males that shared songs during the

1970-80 season (group B; Fig. 7.5). During the second and third breeding seasons, two males sang this subdialect theme and the subdialect finally disappeared during the fourth season. These observations of subdialects thus support only the prediction of the social adaptation hypothesis.

(F) Role of Social Interaction

Here a prediction is made solely by the social adaptation hypothesis which states that only song sharing males interact socially. Results from this study clearly indicate that males who interact vocally share song patterns. I also found that birds who had adjacent territories but did not interact had dissimilar songs; an observation which supports the model of social adaptation.

(G) Behavioural Function of Song

The hypothesis of racial specialization assumes that songs play an important role in mate attraction and that a female chooses a mate who sings her father's song. In contrast, the social adaptation hypothesis predicts that songs will function primarily in intrasexual social interactions. The historical model makes no prediction in this aspect. The results shown in Chapter 6 (p. 68) strongly suggest that brown creeper song functions primarily in male/male interactions and not in the attraction of prospective mates. This is consistent with the prediction of the social adaptation hypothesis.

(H) Behavioural Development of Song

The prediction of the racial specialization model is that a male learns his song from his father and that once acquired it cannot be modified. The hypothesis of social adaptation states that males learn songs from males with whom they socially interact and that song is learned throughout life. The historical hypothesis offers no firm predictions on song development. My findings support the social

adaptation model. However, males showed little ability to modify their songs once they had been stabilized. Although this appears to support the racial hypothesis, I feel that the inability of male brown creepers to modify their songs after song stabilization is due to the sedentary nature of adult birds. Brown creeper males may not need to be able to vary songs because it is unlikely they will change territories.

CONCLUSIONS

The results of this examination suggest that there is little support for the racial specialization hypothesis and where this hypothesis was upheld so was the historical one (Table 7.9). Observations from this study did support the historical and social adaptation hypotheses. However, each could be describing song variation at different levels. I propose that at the dialect or macro-geographic level, the historical hypothesis is the most appropriate to explain the development of the eight dialects studied. In this hypothesis, dialect populations are seen as isolated demes, each developing a different song pattern through the accumulation of random song changes. Thus, dialects have no adaptive significance but are the product of chance. As I suggested earlier, open farmland or riverbeds may act in some cases as barriers to brown creepers preventing movement of birds between populations. In other situations birds may be capable of crossing these open areas but would not venture out into them to socially interact with a neighbouring male. Without social contact the songs of the birds on either side of the open area would be expected to diverge.

The social adaptation hypothesis, in contrast, appears to best explain the pattern of song variation within populations on the micro-geographic level. Subdialects are the unit of comparison at this level. Within these units, males interact socially and share song

patterns. Between subdialect groups, however, interactions are limited and there is less song sharing. The adaptive significance of song sharing in the brown creeper is that it appears to enable birds to efficiently establish and maintain territorial boundaries (see Chapt. 10).

CHAPTER 8

RESPONSES OF MALE BROWN CREEPERS TO SONGS FROM DIFFERENT LOCALITIES

INTRODUCTION

Brown creepers form song dialects which differ principally in the morphology of notes composing the songs and in the general pattern of songs. These dialects, however, varied in their degree of similarity to others (Chapt. 7, p. 117). For example, the numbers of song characters that differed significantly between the Lake Rotorua and West Bank dialects indicated that they were more alike than the Lake Rotorua and Kowhai Bush dialects (Table 7.5).

In a number of song bird species that possess song dialects, males respond less to playback of a foreign dialect than to a local one (e.g. great tit, Gompertz 1961; cardinal [Cardinalis cardinalis], Lemon 1967; Indian hill mynah [Gracula religiosa], Bertram 1970; white-crowned sparrow, Milligan and Verner 1971, Petrinovich and Patterson 1981; song sparrow, Harris and Lemon 1974). It has been suggested, that this results from a tendency for foreign dialects to be physically different from a male's dialect and thus not immediately recognised as a song of a conspecific (Harris and Lemon 1974). If this is the case, then a male should respond less to a song that is very different from his own than one that is more similar. To test this hypothesis I asked the following question: Does the degree of difference, as measured by the number of song characters that vary significantly between dialects, influence the intensity of the response by males? Apparently, this hypothesis has not been previously investigated (see Petrinovich and Patterson 1981).

RESULTS

PLAYBACK EXPERIMENT 1

The 20 males from Kowhai Bush were played 3-min tape recordings of both their local dialect and the Lake Rotorua dialect followed by 3 min when the recorder was turned off but was still in position. In this experiment the birds responded to playback of either the Lake Rotorua or the Kowhai Bush themes but not to the control (Table 8.1). Statistical differences resulted from the lack of response to the control condition.

Males responded more to the local Kowhai Bush theme than to the song from Lake Rotorua in five of the six response categories (Table 8.1). When hearing their own dialect, these birds sang more songs and started singing sooner. In comparison to their reaction to the Lake Rotorua dialect, they approached to within 5 m of the loudspeaker quicker and closer before and after playback in response to their local theme. After playback, a greater mean number of songs, but not a significant one, was sung by the males answering to their own dialect.

A minute-by-minute analysis of the mean number of songs sung in response to playback of both the local and foreign songs shows that the number of songs increased steadily during the first 3 min (Fig. 8.1). Throughout this period, however, more songs were sung in reply to the local theme than to the foreign song. In both cases, once the playback tape was turned off the bird's singing activity dropped off dramatically.

PLAYBACK EXPERIMENT 2

Twelve Lake Rotorua males were played their own dialect and the Kowhai bush song in the same manner as in Experiment 1. The birds again responded strongly to either of the two song dialects. The one exception to this was the number of songs sung after the playback stopped.

Table 8.1 Responses of 20 Kowhai Bush males to no playback (control), playback of a Lake Rotorua song (foreign) and playback of a Kowhai Bush song (local).

Response Category			Condition		
			Control	Foreign Song	Local Song
Number of songs sung during playback	$\bar{X}$		0.0	7.8	15.1
	X_r^2[a]	=	34.9	$p < 0.005$	
	T[b]	=	17.5 (n=20)	$p < 0.005$	
Number of songs sung after playback	$\bar{X}$		0.0	0.9	1.2
	X_r^2	=	10.2	$0.005 < p < 0.001$	
	T	=	60.0 (n=17)	$p > 0.05$	
Latency in singing sec.	$\bar{X}$		180.0	79.0	26.4
	X_r^2	=	33.6	$p < 0.005$	
	T	=	15.0 (n=20)	$p < 0.005$	
Latency in approach sec.	$\bar{X}$		180.0	88.1	29.9
	X_r^2	=	38.1	$p < 0.005$	
	T	=	0.0 (n=20)	$p < 0.005$	
Approach rank during playback	$\bar{X}$		0.0	1.4	2.4
	X_r^2	=	31.3	$p < 0.005$	
	T	=	0.0 (n=12)	$p < 0.005$	
Approach rank after playback	$\bar{X}$		0.0	0.4	1.0
	X_r^2	=	12.7	$p < 0.005$	
	T	=	0.0 (n=7)	$p < 0.01$	

[a] Friedman two-way analysis of variance of all three conditions.

[b] Wilcoxon matched-pairs signed-ranks test of foreign versus local songs.

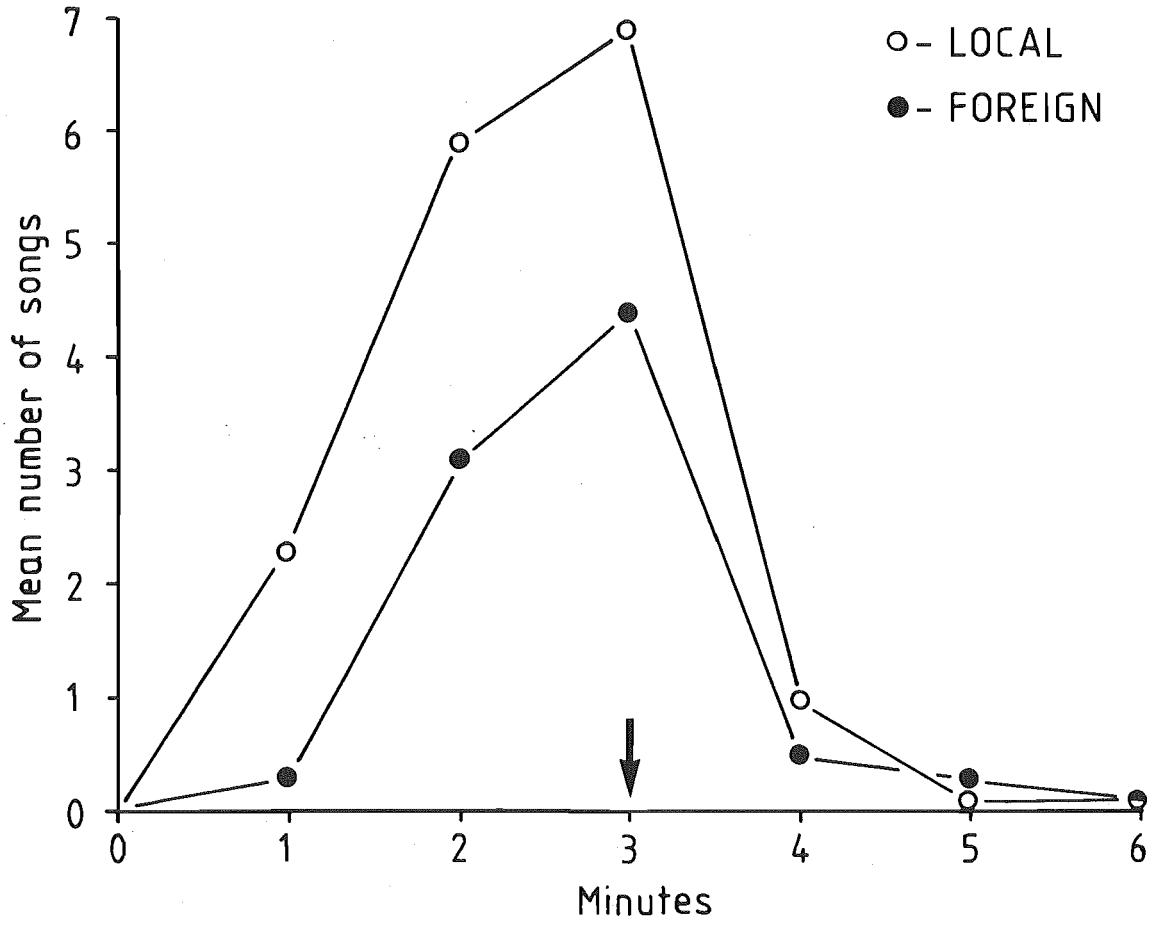

Fig. 8.1. Experiment 1: mean number of songs sung in response to local and foreign songs during each minute of observation. Arrow indicates when playback recordings were turned off.

In three of the response categories, the males reacted more vigorously to their own dialect than to the foreign one (Table 8.2). These categories were number of songs sung during the first 3 min, time until singing commenced, and time to approach within 5 m of the loudspeaker.

During the first 3 min of playback the number of songs in reply to the local dialect was always greater than to the foreign one (Fig. 8.2). Singing was reduced to near zero during the second 3 min period after both dialects had been played.

PLAYBACK EXPERIMENT 3

Responses of 13 Kowhai Bush males to the three test conditions indicated that these males also reacted more intensely to either Kowhai Bush or West Bank themes than to the control (Table 8.3). This trend was statistically significant for five of the six response categories. Only the number of songs sung after the playback period did not follow this tendency.

The birds responded more to the local dialect in half of the response categories. Males sang more often during the first 3 min of the experiment and responded by singing and approaching within 5 m of the loudspeaker more quickly when played the local Kowhai Bush dialect.

As in the previous experiments, the number of songs sung during the playback period in reply to the local theme was higher than to that of the foreign theme (Fig. 8.3). The bird's singing activity rapidly declined when the playback tape was turned off.

PLAYBACK EXPERIMENT 4

The results of this experiment conducted at Lake Rotorua indicate that the 14 males tested responded far greater to playback of the Lake

Table 8.2 Responses of 12 Lake Rotorua males to no playback (control), playback of a Kowhai Bush song (foreign) and playback of a Lake Rotorua song (local).

Response Category			Condition		
			Control	Foreign Song	Local Song
Number of songs 1st 3 min.	$\bar{X}$		0.0	5.1	10.5
	$X_r^{2\,a}$	=	19.5	$p < 0.005$	
	T^b	=	7 (n=12)	$p < 0.005$	
Number of songs 2nd 3 min.	$\bar{X}$		0.0	0.5	0.5
	X_r^2	=	2.6	$p > 0.05$	
	T	=	-*		
Latency of song	$\bar{X}$		180.0	105.6	56.4
	X_r^2	=	19.5	$p < 0.005$	
	T	=	11 (n=12)	$0.01 < p < 0.025$	
Latency of approach	$\bar{X}$		180.0	106.8	58.8
	X_r^2		20.0	$p < 0.005$	
	T	=	8.5 (n=11)	$0.01 < p < 0.025$	
Approach rank during 1st 3 min.	$\bar{X}$		0.0	1.1	2.3
	X_r^2		13.6	$p < 0.005$	
	T	=	6.0 (n=8)	$p > 0.05$	
Approach rank during 2nd 3 min.	$\bar{X}$		0.0	0.8	1.2
	X_r^2		7.5	$0.01 < p < 0.025$	
	T	=	8.0 (n=7)	$p > 0.05$	

[a] Friedman two-way analysis of variance of all three conditions.

[b] Wilcoxon matched-pairs signed-ranks test of foreign versus local songs.

* T not calculated because the Friedman two-way analysis of variance did not reveal a significant difference between the three conditions.

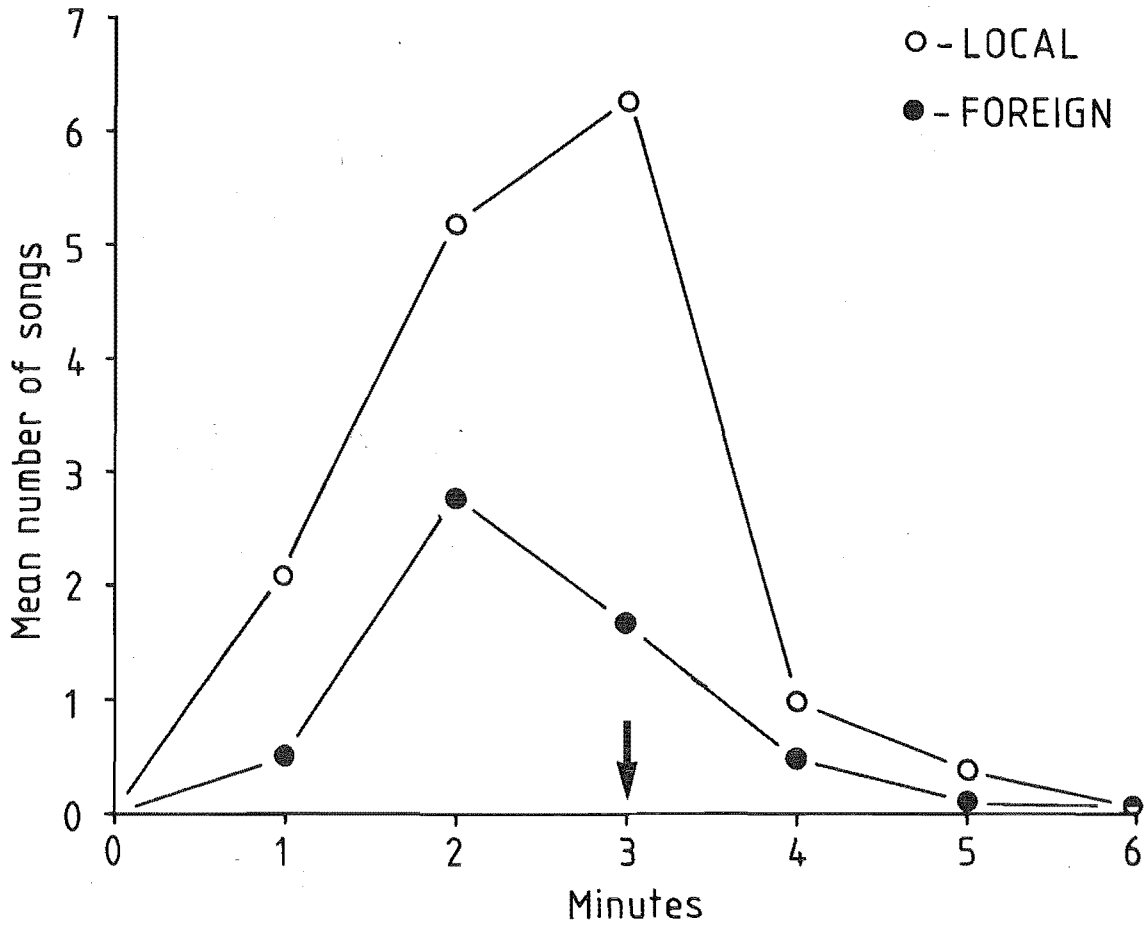

Fig. 8.2. Experiment 2: mean number of songs sung in response to local and foreign songs during each minute of observation. Arrow indicates when playback recordings were turned off.

Table 8.3 Responses of 13 Kowhai Bush males to no playback (control), playback of a West Bank song (foreign) and playback of a Kowhai Bush song (local).

Response Category		Condition		
		Control	Foreign Song	Local Song
Number of songs 1st 3 min.	$\bar{X}$	0.0	5.0	13.6
	X_r^{2a} =	18.6	$p < 0.005$	
	T^b =	3.0 (n=13)	$p < 0.005$	
Number of songs 2nd 3 min.	$\bar{X}$	0.0	0.6	1.4
	X_r^2 =	1.6	$p > 0.05$	
	T =	-*		
Latency of song	$\bar{X}$	180	115.4	42.7
	X_r^2 =	20.5	$p < 0.005$	
	T =	3.0 (n=13)	$p < 0.005$	
Latency of approach	$\bar{X}$	180	117.5	62.7
	X_r^2 =	18.0	$p < 0.005$	
	T =	12.0 (n=13)	$0.005 < p < 0.01$	
Approach rank during 1st 3 min.	$\bar{X}$	0.0	1.2	2.0
	X_r^2 =	18.0	$p < 0.005$	
	T =	7.0 (n=9)	$0.025 < p < 0.05$	
Approach rank during 2nd 3 min.	$\bar{X}$	0.0	0.7	1.4
	X_r^2 =	11.8	$p < 0.005$	
	T =	11.5 (n=10)	$p > 0.05$	

[a] Friedman two-way analysis of variance of all three conditions.

[b] Wilcoxon matched-pairs signed-ranks test of foreign versus local songs.

* T not calculated because the Friedman two-way analysis of variance did not reveal a significant difference between the three conditions.

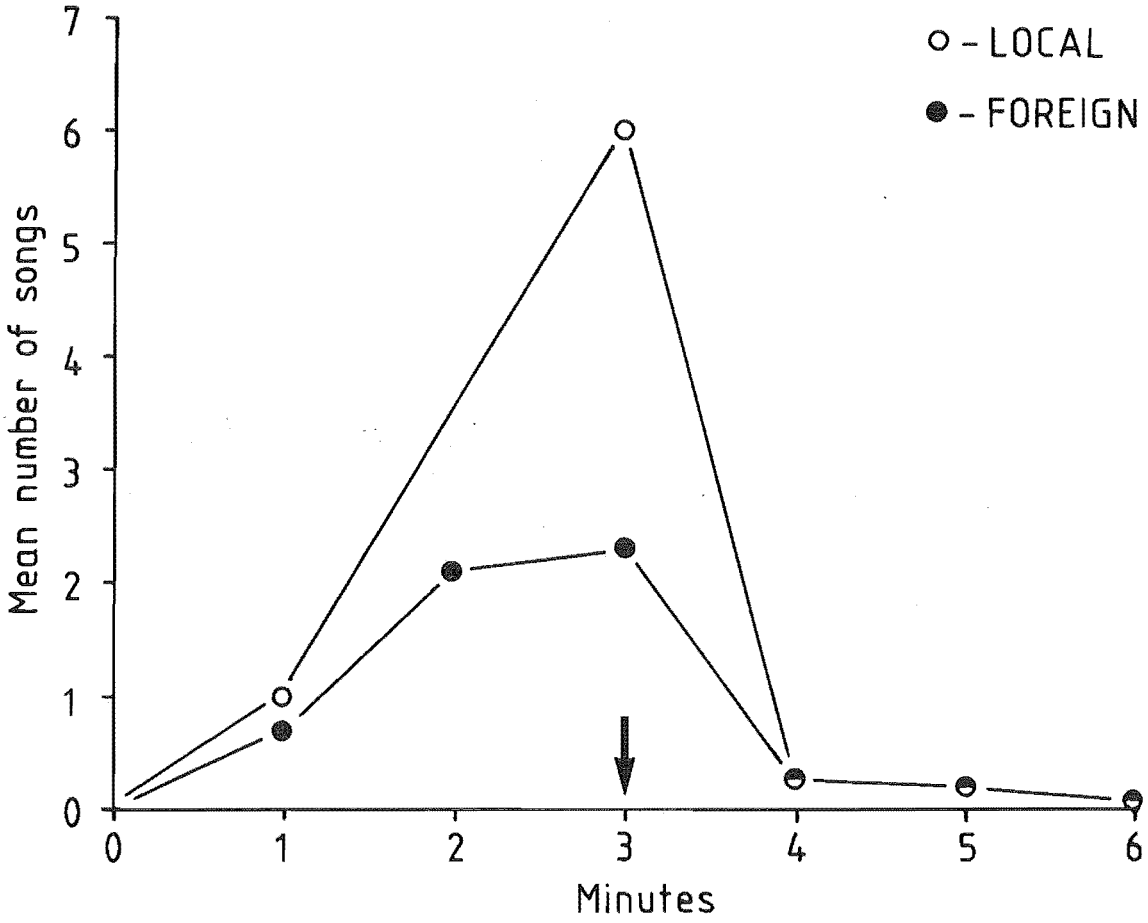

Fig. 8.3. Experiment 3: mean number of songs sung in response to local and foreign songs during each minute of observation. Arrow indicates when playback recordings were turned off.

Rotorua and West Bank themes than to the control in five of the response categories (Table 8.4). However, when responses to the local and foreign dialects were compared there were no differences except in the category of latency of approach to the loudspeaker.

In contrast to the previous three experiments, the male's singing activity increased at a similar rate regardless of the dialect that was played (Fig. 8.4). During the last minute of the playback period the males sang slightly more songs after hearing their local theme than to the foreign song.

DISCUSSION

The results of this study clearly indicate that during playback of the species' specific song, males responded; but once the stimulus was turned off they stopped singing and did not remain close to the loudspeaker. This cessation of singing is very unusual and as far as I am aware has not been reported before in passerines.

In other species which have been tested with these experiments, males showed a residual effect to playback and continued to sing, display and stay close to the loudspeaker after the playback song was turned off. This effect has been noted in the cardinal (Lemon 1967), white-throated sparrow (Zonotrichia albicollis, Falls 1969), white-crowned sparrow (Milligan and Verner 1971, Petrinovich and Patterson 1981) and indigo bunting (Passerina cyanea, Emlen 1972). In the brown creeper, however, vocal stimulation of another singing male appeared to be required to bring on prolonged singing activity and with an absence of the stimulus, the birds quickly ceased singing and moved away. These results suggest that male-male singing in the brown creeper is a highly social activity (see Chapt. 10).

The results from the first three experiments indicate that male

Table 8.4 Responses of 14 Lake Rotorua males to no playback (control), playback of a West Bank song (foreign) and playback of a Lake Rotorua song (local).

Response Category			Condition		
			Control	Foreign Song	Local Song
Number of Songs 1st 3 min.	$\bar{X}$		0.0	9.4	10.8
	X_r^2[a]		21.3	p <0.005	
	T[b]	=	25.5 (n=13)	p >0.05	
Number of songs 2nd 3 min.	$\bar{X}$		0.0	0.6	0.6
	X_r^2		3.3	p >0.05	
	T	=	-*		
Latency of song	$\bar{X}$		180.0	55.0	22.9
	X_r^2		21.6	p <0.005	
	T	=	30.5 (n=14)	p >0.05	
Latency of approach	$\bar{X}$		180.0	59.9	24.8
	X_r^2		21.6	p <0.005	
	T	=	16.5 (n=14)	0.01 < p <0.025	
Approach rank during 1st 3 min.	$\bar{X}$		0.0	2.0	2.1
	X_r^2		18.2	p <0.005	
	T	=	12.5 (n=7)	p >0.05	
Approach rank during 2nd 3 min.	$\bar{X}$		0.0	1.1	0.9
	X_r^2		8.8	0.01 < p <0.025	
	T	=	3.5 (n=4)	p >0.05	

[a] Friedman two-way analysis of variance of all three conditions.

[b] Wilcoxon matched-pairs signed-ranks test of foreign versus local songs.

* T not calculated because the Friedman two-way analysis of variance did not reveal a significant difference between the three conditions.

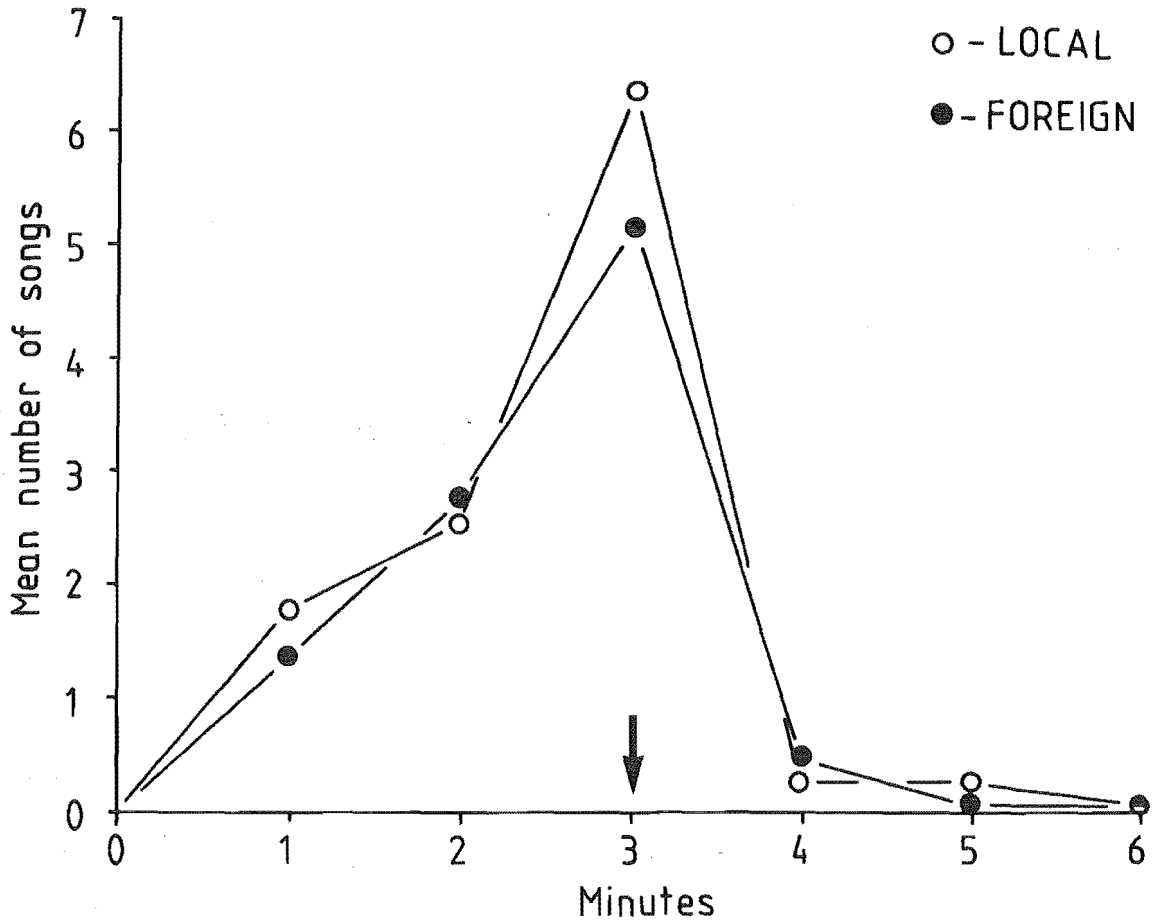

Fig. 8.4. Experiment 4: mean number of songs sung in response to local and foreign songs during each minute of observation. Arrow indicates when playback recordings were turned off.

brown creepers respond less to foreign dialects. These findings are in agreement with those from several other species (Gompertz 1961, Lemon 1967, Bertram 1970, Harris and Lemon 1974, Petrinovich and Patterson 1981).

The degree of difference between the song heard and the receiver's own song may account for differences in the way male brown creepers respond to local and foreign dialects. The more similar the songs, the closer to equal the response level. For example, in the first three experiments, as mentioned above, males reacted stronger to the local dialect than to the foreign one. The Kowhai Bush and the Lake Rotorua dialects differed significantly by 14 of the 16 song characters while Kowhai Bush and West Bank dialects differed in 11 (Chapt. 7, Table 7.5). Thus these dialects differed in a number of ways. In contrast to this, in Experiment 4, Lake Rotorua males appeared to be unable to discriminate between the local and the West Bank theme. These two dialects differed in only three of the 16 song characters (Chapt.9).

The degree of difference between song dialects may be affected by a number of factors such as the distances between localities, the length of time adjacent populations have been separated and the rate of change in the morphology of songs. The Kowhai River, which separates Kowhai Bush from West Bank and Lake Rotorua, has probably flowed in its present location, except for periodic short-term changes due to flooding, for at least several hundred to a thousand years (R.M. Kirk, pers. comm.). If the river forms an effective acoustical or geographical barrier, then there would have been considerable time for songs on both sides to deviate in their morphology. In contrast, West Bank and Lake Rotorua populations are only separated by open farmland which has been there for no longer than 120 years following the first Kaikoura land sale in the 1860s. Thus these two populations did not have as much time to develop major changes in their song morphology.

The brown creeper males' lower response to foreign dialects suggests that strangers have an easier time establishing a territory than local birds. However, in all of the populations I sampled, I found no males singing foreign songs. This may simply be because males do not or are unable to cross the barriers separating populations. Alternatively, I show later (Chapt. 10) that males who sing foreign themes and thus do not share songs with their neighbours are unable to efficiently maintain their territorial boundaries. Thus, foreign males would not be as effective in setting up territories as a local male.

In conclusion, the results of this investigation suggest that the male brown creeper's discrimination of local and foreign songs is based upon the degree of difference between the two themes. The degree of difference between songs sung by males in separated populations is probably determined by the length of time the populations have been apart.

CHAPTER 9

NEIGHBOUR/STRANGER DISCRIMINATION AND INDIVIDUAL RECOGNITION IN THE BROWN CREEPER

INTRODUCTION

Field playback experiments have been used to demonstrate the ability of songbird species, possessing single song repertoires, to discriminate between the songs of neighbours and strangers (e.g. ovenbirds [Seiurus aurocapillus], Weeden and Falls 1959; white-throated sparrows [Zonotrichia albicillis], Falls 1969, Lemon and Harris 1974, Brooks and Falls 1975; indigo buntings [Passerina cyanea], Emlen 1971; field sparrows [Spizella pusilla], Goldman 1973; common yellowthroats [Geothlypis trichos], Wunderle 1978; white-crowned sparrows [Zonotrichia leucophrys]; Baker et al. 1981). In each of these studies, males responded more strongly to the songs of a stranger than to those of a neighbour.

At least two processes, habituation and associative learning, may be involved in the development of discrimination between neighbour's and stranger's songs (Falls 1982). Alcock (1975) defines habituation as the "relatively permanent reduction or elimination of a response in the absence of any overt reward or punishment." In contrast, associative learning as defined by Alcock is a "change in behavior towards a particular stimulus because of past rewards or punishments for reacting a certain way to the object in question." Habituation has been frequently suggested to explain males' decreased reaction towards the song of neighbours (Falls 1982). The proponents of this idea argue that song habituation results from repeated exposure to a neighbour's songs and may be adaptive because it reduces the rate and intensity of conflicts between neighbouring males with established boundaries, also saving energy and lowering risks associated with fighting (Weeden and Falls

1959). Recently, however, Richards (1979) demonstrated that associative learning in the rufous-sided towhee (Pipilo erythrophthalmus) probably plays a significant role in the development of neighbour/stranger discrimination and individual recognition. He discovered that male towhees sometimes develop aberrant songs by mimicking the songs of Carolina wrens (Thryothorus ludovicianus). By using playback experiments he found that towhees with neighbours which sang the aberrant songs responded strongly to playback of these songs, but non-neighbours hardly reacted. To explain these results, Richards suggested that some male towhees learn to recognise the aberrant song and associate it with the appearance of a conspecific. Falls (1982) interpreted the strong responses of neighbouring Eastern and Western meadowlarks (Sturnella magna and S. neglecta) to each other's songs in a similar manner. When living in allopatry, these two species normally do not respond to each others songs. Neighbour/stranger discrimination in red-winged blackbirds has also been proposed as a result of associative learning (Yasukawa et al. 1982).

I conducted two types of playback experiments in order to test the ability of territorial male brown creepers to discriminate between the songs of neighbours and strangers and to recognise the songs of individuals. In the first experiment, I found that male brown creepers discriminate between the songs of neighbours and strangers. Evidence is presented from the second experiment suggesting that associative learning may be involved in this discrimination and that males can recognise individuals by song. The data for this came from experiments conducted in the main study area on neighbours and non-neighbours of a male (MR-RB) who sang the Lake Rotorua theme throughout the experimental period.

RESULTS

MALES' RESPONSES TO SONGS OF NEIGHBOURS, STRANGERS AND THE CONTROL - EXPERIMENT 1

When seven males in Kowhai bush were tested with playback of the song of a neighbour, the song of a stranger and the control, the birds responded more strongly to playback of the two songs than the control when no song was played (Table 9.1). Answers to the stranger's songs were more intense than to those to neighbours in four of the six categories. In general, the males sang more songs during playback, began singing more quickly, made faster approaches to within 5 m of the loudspeaker and stayed closer to the loudspeaker during the second 3-min period of the experiment longer when responding to the stranger's songs. There was no difference in the response of males to the songs of neighbours and strangers in two of the response categories: the number of songs sung in the second 3-min period of the experiment and how close they came to the loudspeaker during playback.

A comparison of the mean number of songs sung in reply to playback of stranger's and neighbour's songs shows that throughout the duration of the experiment males sang more in response to the stranger's than to the neighbour's song (Fig. 9.1). The singing activity of the males also increased during the first 3-min period of the experiment for both songs but then declined during the last 3 min, when playback was turned off.

ASSOCIATIVE LEARNING IN NEIGHBOUR/STRANGER RECOGNITION - EXPERIMENT 2

Six non-neighbours of the transferred male MR-RB, reacted more intensely to playback of a local Kowhai Bush song than to MR-RB's songs in all three response categories (Table 9.2; Wilcoxon signed-ranks test; $P < 0.025$). However, the responses of these males to the songs of a second Lake Rotorua male were not different from those towards MR-RB's songs (Wilcoxon signed-ranks test; $P > 0.05$).

Table 9.1 Responses of seven males to conditions of no playback (control), playback of a neighbour's song, and playback of a stranger's song.

Response Category			Condition		
			Control	Neighbour's Song	Stranger's Song
Number of songs during playback	$\bar{X}$		0.0	10.4	15.7
	$X_r^{2\,a}$	=	13.1	$p < 0.005$	
	T^b	=	0 (n=7)	$p < 0.01$	
Number of songs after playback	$\bar{X}$		0.0	0.1	1.1
	X_r^2	=	7.7	$0.01 < p < 0.025$	
	T	=	2.5 (n=5)	$p > 0.05$	
Latency of singing sec.	$\bar{X}$		180.0	88.8	28.3
	X_r^2	=	13.1	$p < 0.005$	
	T	=	0 (n=7)	$p < 0.01$	
Latency of approach sec.	$\bar{X}$		180.0	89.0	32.7
	X_r^2	=	13.1	$p < 0.005$	
	T	=	0 (n=7)	$p < 0.01$	
Approach rank during playback	$\bar{X}$		0.0	2.4	2.4
	X_r^2	=	8.7	$0.01 < p < 0.025$	
	T	=	4.5 (n=5)	$p > 0.05$	
Approach rank after playback	$\bar{X}$		0.0	0.4	1.6
	X_r^2	=	11.1	$p < 0.005$	
	T	=	0 (n=6)	$p < 0.025$	

[a] Friedman two-way analysis of variance of all three conditions.

[b] Wilcoxon matched-pairs signed-ranks test of neighbours' versus strangers' songs.

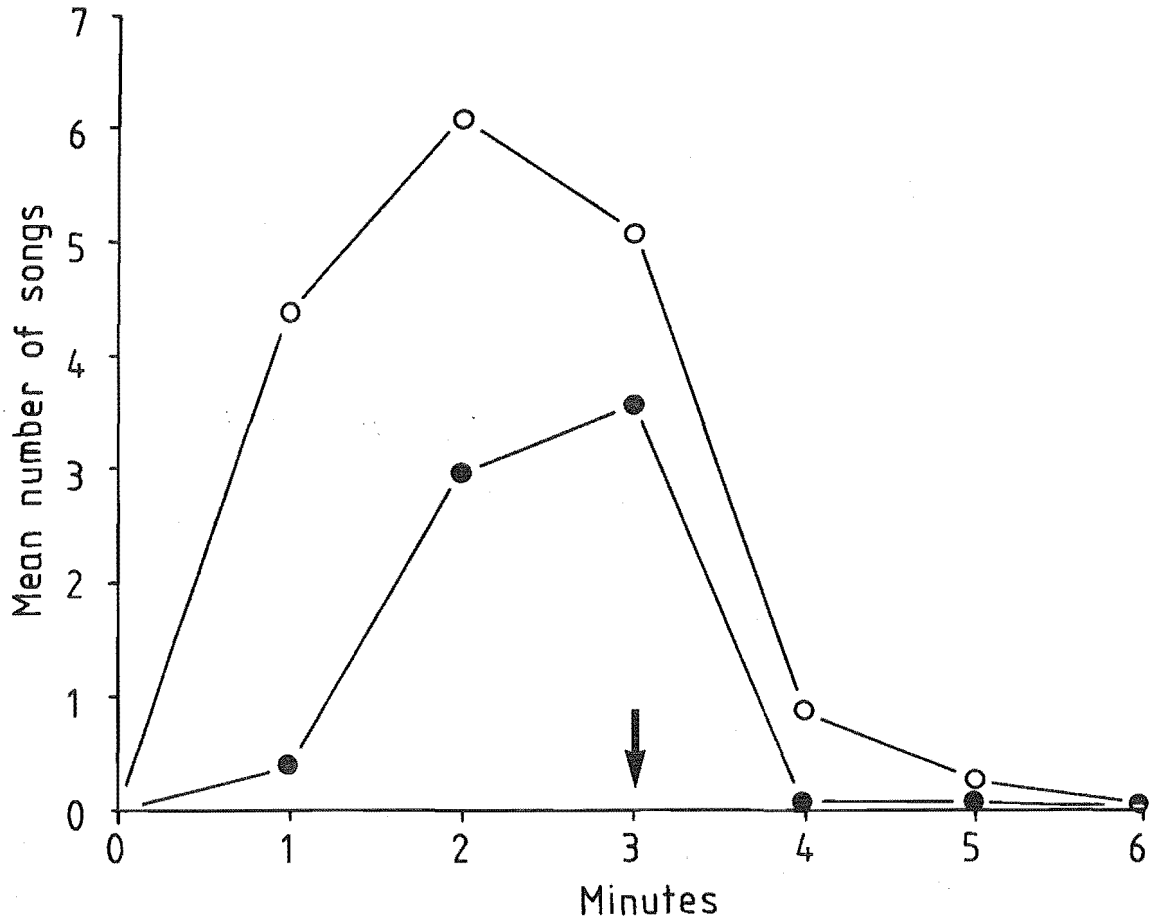

Fig. 9.1. Mean number of songs sung in response to the songs of neighbours (solid circles) and strangers (open circles) during each minute of observation. Arrow indicates when playback recordings were turned off.

Table 9.2 Responses of the non-neighbours of a male transferred from Lake Rotorua into Kowhai Bush (MR-RB) to playback of a local Kowhai Bush song, the transferred male's song, and another Lake Rotorua male's song.

		Response Categories		
Presentation	N	Number of songs	Latency of singing	Approach rank
Local song	6	15.3	25.4	2.7
MR-RB's song	6	7.5	80.0	1.3
Lake Rotorua song	6	6.8	92.8	1.0

Table 9.3 Responses of the neighbours of a male transferred from Lake Rotorua into Kowhai Bush (MR-RB) to playback of a local Kowhai Bush song, the transferred male's song and another Lake Rotorua male's song.

		Response Categories		
Presentation	N	Number of songs	Latency of singing	Approach rank
Local song	6	12.4	24.8	2.6
MR-RB's song	6	11.0	25.3	2.4
Lake Rotorua song	6	5.1	105.6	1.1

In part two of this experiment, the neighbours of MR-RB did not respond differently to playback of MR-RB's song and the song of a local Kowhai Bush male (Table 9.3; Wilcoxon signed-ranks test; $P > 0.05$). However, they did respond less to playback of a song from a second Lake Rotorua male (Wilcoxon signed-ranks test; $P < 0.025$).

DISCUSSION

The results of Experiment 1 clearly demonstrate that male brown creepers react more intensely to the song of an unfamiliar non-neighbour from the same dialect population than to a familiar neighbour. These results are in agreement with those obtained for other species with single song repertoires (review: Falls 1982). It has been suggested that this difference in the male's response towards the songs of neighbours and strangers may be a general phenomenon in species like the brown creeper with small song repertoires (Falls 1982). Of the two processes by which neighbour/stranger discrimination is thought to have developed in song birds, habituation has received the greatest attention from researchers. Habituation to specific stimuli has been experimentally induced in a number of species. For instance, Petrinovich and Peeke (1973) demonstrated that white-crowned sparrows readily become used to specific song patterns. During this investigation I noted that male brown creepers reacted strongly and quickly to playback songs when they were first presented but this initial response declined with repeated exposure. If, however, a new song from the same dialect which the males had not heard previously was substituted for the first, the bird's response was again heightened. It appears from these observations that in this species the birds can become habituated to a particular song pattern after repeated exposure.

Although it is possible that habituation to song occurs in the wild, I suggest that the experimental conditions described above do not accurately reflect what occurs naturally between two neighbouring male brown creepers. I caused the birds to become accustomed to a song by playing it repeatedly and thus there was little or none of the normal variation between song repetitions. This same procedure of playing the same song repeatedly has been employed by other investigators of avian

habituation (e.g. Petrinovich and Peeke 1973; Patterson and Petrinovich 1979; Petrinovich and Patterson 1979, 1980).

The songs of male brown creepers are stereotyped but exhibit a measurable amount of variation between repetitions; coefficients of variation for several song characters that were measured ranged from 0.32 -10.0% (Chapter 7, Table 7.1). Furthermore, males are not continuous singers but are often silent for long periods (Chapter 6, p. 67). Even when vocally interacting with neighbours, males interrupt their singing with bouts of calling and feeding (Chapters 6 and 10). The variation between song repetitions and the discontinuous singing pattern of male brown creepers may, I suggest, prevent habituation or at least delay its development.

In Experiment 2, I found that Kowhai Bush males who were neighbours of a male who sang the Lake Rotorua theme had as strong a reaction to this foreign song as to songs from Kowhai Bush dialect. Non-neighbours of the transferred male responded less to his song than to the local Kowhai Bush song. These results strongly suggest that associative learning, and not habituation, is responsible for neighbour/stranger discrimination in the brown creeper. In most investigations of neighbour/stranger discrimination males responded less to the songs of neighbours than to the songs of strangers and habituation has been offered as an explanation. However, here I have demonstrated a stronger response by neighbours than by distant birds, thus confirming the role of associative learning in the discrimination.

The results of this experiment also suggest that male brown creepers learn a specific song and not a generalized one through association. Neighbours of MR-RB responded more strongly to MR-RB's song than to the song of another male from Lake Rotorua. This demonstrates that male brown creepers are capable of individual recognition. In two other studies (Wiley and Wiley 1977, Falls and Brooks 1975) the ability

to recognise individuals has been reported. In both, the birds could recognise and associate the songs of each neighbour with the location from which the neighbour usually sang. They responded no differently to a neighbour's song played from a wrong location than to a stranger's song. If neighbours' songs were only recognised as a class of familiar sounds, then it should not matter at which part of the boundary the song is played.

Individual recognition is to be expected between birds that are in continuous or repeated contact (Falls 1982). Brown creepers are long lived and remain on the same territory for several seasons (Chapter 4) and probably interact with the same birds for several years. When individuals are recognised the behaviour of these familiar birds are more predictable and conflicts between known birds may be fundamentally different from those involving strangers. In encounters between birds who know one another, deception may be replaced by known asymmetries between the contestants based upon past experience (van Rhijn and Vodegel 1980).

If male brown creepers recognise the songs of individuals, then which features of the song pattern are most likely to be important in individual recognition? Sonagrams of six neighbouring males within the main study area show that to the left of the vertical line all the songs are very similar in both the overall pattern of the notes and in the morphology of individual notes (Fig. 9.2). Some individual differences exist in the first one or two introductory notes but these are also variable within individuals and are therefore probably of little value in individual recognition. To the right of the vertical line, songs differ markedly in both the morphology and pattern of the notes. I suggest that it is this portion of the brown creeper song which is important in individual recognition. To test this hypothesis it would be necessary to alter various features of the song and see if birds still recognised the

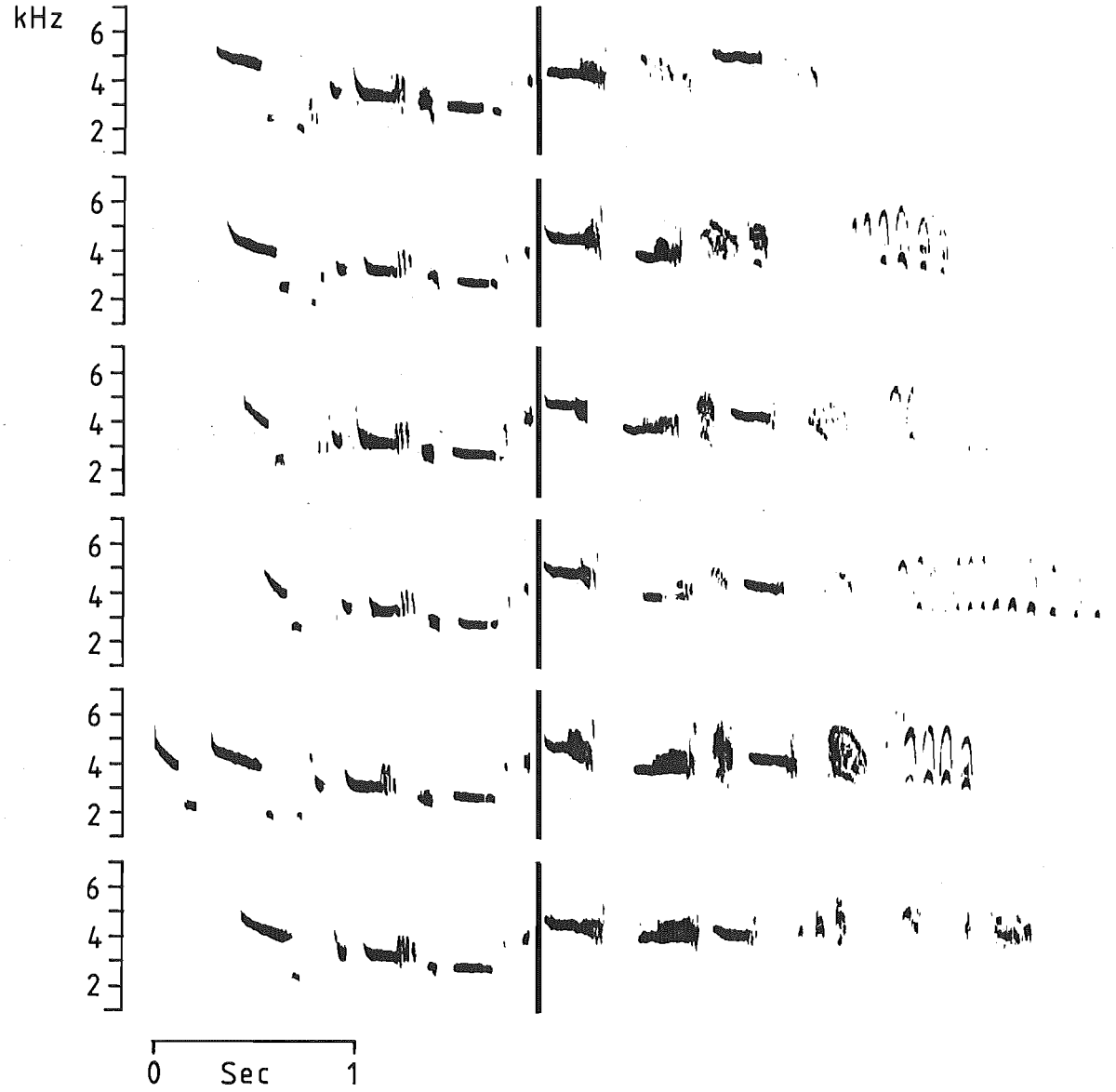

Fig. 9.2. Sonagrams of the songs and interludes of six neighbouring males in Kowhai Bush. Left of heavy vertical line there is little variation between males but the portion to the right shows individual distinctiveness.

altered songs as coming from a particular individual.

In summary, male brown creepers respond differently to the songs of neighbours and those of strangers, reacting more intensely to the unfamiliar song of the latter. The brown creeper probably learns to discriminate between such songs through association. During social interactions, males may learn who their neighbours are through repeated exposure to their songs. Eventually, males reduce their aggression towards those males with whom they share territorial boundaries. Furthermore, the songs learned through association are specific to certain neighbours and are not generalized. Thus male brown creepers recognise the songs of individuals and the terminal section of male song may be important in this recognition.

CHAPTER 10

UNISON SINGING AND ITS FUNCTION IN TERRITORIAL DEFENSE

INTRODUCTION

The singing behaviour of songbirds plays an important role in the establishment and maintenance of territorial boundaries (Marler 1956, Armstrong 1963, Krebs et al. 1978, Falls 1978). This is thought to be accomplished by the transmission of information regarding territorial ownership (review: Falls 1978). However, up until now, it has remained unclear whether the information transmitted is encoded in the song pattern itself or whether the vocal interactions between males acts as a necessary component (Todt 1981).

The most common form of vocal interaction between two males occurs when they temporally alternate their songs (Marler 1956; Falls 1969, 1978). This response, frequently called alternate singing, has been interpreted as a way to avoid the mutual masking of songs (Bremond 1977, Wasserman 1977). Furthermore, since physiological constraints on avian hearing during singing may prevent a bird's recognition of the sound pattern of another conspecific (Hultsch and Todt 1982), alternate singing may be a mechanism which allows two birds to hear each other as they interact vocally (Wasserman 1977).

In a few species of birds, however, interacting males superimpose their songs in what Todt (1981) refers to as overlap singing. Examples include the European nightingale (Luscinia megarhynchos; Todt 1971), the roller canary (Serinus canaria; Wolffgramm 1975), the redstart (Phoenicurus phoenicurus; Thimm 1976), and the European blackbird (Dabelsteen 1981). Todt (1981) concluded that overlap singing in blackbirds functions as a form of vocal threat possibly playing a role in the regulation of distances between neighbouring males.

During my study of the singing behaviour of male brown creepers, I discovered a unique form of overlap singing that occurred during territorial disputes which I call unison singing (see Appendix 3). Since few studies of overlap singing have been undertaken, I felt an investigation of this behaviour as found in the brown creeper would be productive. My aims were first, to describe this unusual behaviour precisely and, second, to study how unison singing is used in territorial communication. This second goal was accomplished by answering the following questions:

1) Did males vary the number of songs that they overlapped and did this correlate with the intensity of the interaction?
2) Were the delays between the songs of the two interacting males random in length or were certain delays preferred?
3) Did individuals show a preference for singing first or second during a dispute?
4) Some males shortened their songs when unison singing. What was the significance of this behaviour? To answer this question I asked three additional questions. (a) During disputes, when did truncation occur? (b) Did the same male truncate his song throughout a bout? (c) Were leaders or followers more likely to truncate their song?

Finally, since neighbouring males that sing in unison have very similar song patterns (Chapt. 7), I studied the functional significance of song sharing in the brown creeper and attempted to determine its role in male/male communication.

RESULTS

DESCRIPTION OF UNISON SINGING

Each of the over 60 unison singing bouts observed had a similar

general pattern. Bouts commenced when two or sometimes three neighbouring males were attracted to their common territorial boundary by one of the males singing or calling near the border. Those few songs sung at this stage were usually given in strings (Chapt. 6) with overlapping of songs avoided. When the males got within 1-2 m of each other singing activity increased and they began singing only single songs (Chapt. 6). At this point each male rapidly responded to the other's song which often resulted in the overlap of the two songs. A sonagram of two overlapping songs is presented in Fig. 10.1A and B. Such pairs will be referred to as a song dyad. I call the first male to sing the vocal leader and the other the follower. The delay in the response of the follower is the response delay.

Unison singing bouts lasted 14.2 ± 3.1 min (n=40; range=10-20 min) and ended abruptly when the males were 3-4 m apart. Once singing had ceased the two birds gradually moved away from the boundary and returned to their respective territories.

Besides overlapping their songs, interacting males coordinated their movements, performing a display that will be referred to as "dancing". Dancing was similar to the "walk-in-line" behaviour performed by many species (review: Rich 1983). When dancing, one of the males advanced towards the other in short hops while the other retreated by hopping backwards; the two birds thereby moving together. They both faced each other and kept 10-20 cm apart throughout the dance, their feathers sleeked and tails, bodies and heads held low (Chapt. 6; Fig. 6.8B). Tail feathers were only rarely spread and the wings were occasionally fluttered.

During bouts of unison singing the participants sometimes ceased all singing and dancing and began to forage together (whether or not food was actually captured could not be determined). After a variable interval, the males suddenly began to dance and unison sing again.

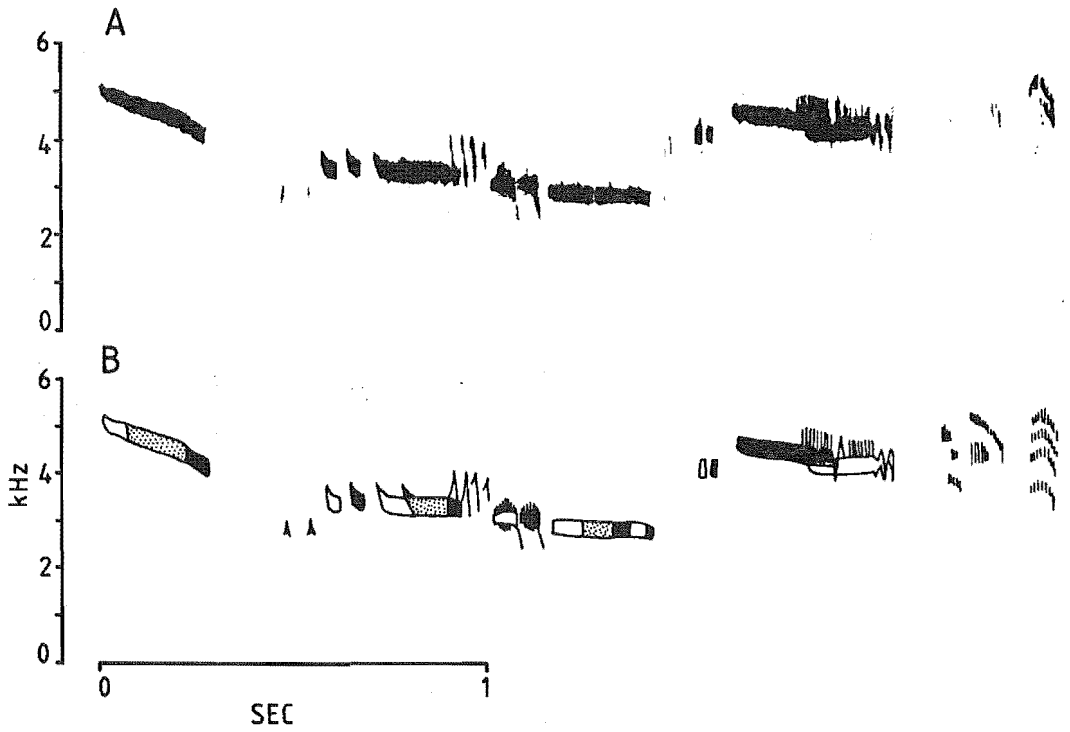

Fig. 10.1. A. Sonagram showing the songs of two males singing in unison (dyad). B. Drawing from sonagram (A) indicating the contribution to dyad by each participant. Open notes are those from first male's song and solid ones are the second male's. Stippled areas indicate parts of notes that have been overlapped.

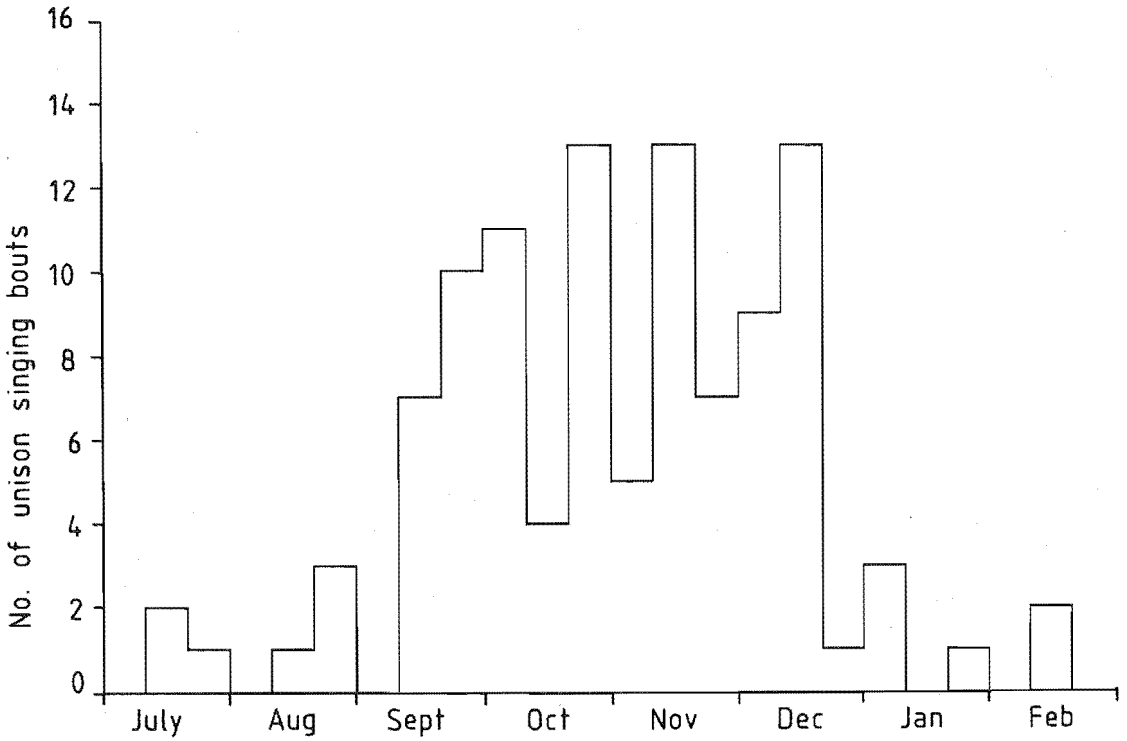

Fig. 10.2. Number of unison singing bouts heard during each month from July 1981 to February 1982. Months are divided into three equal time periods.

Early in the breeding season, before incubation had commenced, females were often present during territorial disputes. While the males sang in unison, the females either flew around the interacting males giving chatter calls (Chapter 6, pp. 75-76) or sang duets with their mates. Occasionally, females chased the females from neighbouring territories if they crossed territorial boundaries. However, in most cases females remained 1-3 m from the interacting males.

The number of unison singing interactions heard per week between July 1981 and February 1982 increased markedly in late-August with most interactions occurring between mid-September and mid-December (Fig. 10.2). From mid-December until February unison singing was only heard occasionally.

Peaks in unison singing activity occurred in early-October, late-October, mid-November and mid-December. The first peak coincided with the commencement of breeding and the adjustment to territorial

boundaries that occur at that time with young males setting up territories. The remaining three peaks probably resulted when breeding pairs changed nest sites for replacement or second clutches. Following these shifts, pairs often utilized different portions of their territories and this sometimes resulted in interactions with neighbours with whom they had not previously come into contact. If this occurred, territorial boundaries with these new neighbours were established or redefined with a subsequent increase in singing activity.

ADJUSTMENTS TO THE SINGING BEHAVIOUR OF MALES

Variation in the Number of Songs Overlapped

The number of playback songs overlapped by each of the 10 males was similar within each playback location (G-test; $P>0.05$) and therefore the results were pooled (Table 10.1). The number of playback songs which the males overlapped varied markedly depending on the placement of the loudspeaker ($G=120.32$; $P<0.005$). When the loudspeaker was placed in the centre of the territory the subject overlapped 81.2% of the songs; while 71.2% were overlapped when the loudspeaker was near the territorial boundary. No songs were overlapped when the loudspeaker was 5 m outside the territory.

Table 10.1 Number of songs played from three different locations that were temporally overlapped by 10 males.

	Centre Territory	Territorial Boundary	Outside Territory
Overlapped	112 (81.2%)	84 (71.2%)	0 (0.0%)
Not overlapped	26	34	48

Adjustments made to the timing of responses

The temporal delays in the onset of singing of one male relative to that of the other during unison singing bouts were not randomly distributed but were bimodal (Fig. 10.3). Many response delays were rapid (0.23 ± 0.116 s; range = 0.04–0.43 s) while others were slower (0.99 ± 0.236 s; range = 0.74–1.54 s).

Observations made while recording unison singing bouts revealed that when males responded rapidly they were spacially closer together and facing each other. They reacted quickly when 0.5 ± 0.25 m (n=23) apart while males that responded slowly were 2.4 ± 0.50 m (n=18).

Individual Preferences for Either Leader or Follower Roles

During each dyad one male began singing and was the vocal leader while the other male who responded was the vocal follower. In nine of the 10 unison singing bouts examined no clear preference for one role over the other was shown by either participant (Table 10.2). For example, during a dispute between M-WW and MW-YY, M-WW was the leader in 9 dyads while MW-YY led in 14. However, during an interaction between M-R and UB-M2, UB-M2 demonstrated a strong preference to lead and M-R to follow. This interaction took place on 7 October 1982, well within M-R's territory. In comparison, the other nine bouts listed in Table 10.1 occurred on or near territorial boundaries.

Song Truncation

Of the ten unison singing bouts analysed, the total time each bout lasted was subdivided into three equal time periods: early, middle and late. No truncated songs were found in the early period, 17 (10.5%) in the middle period and 145 (89.5%) in the late time period. Thus, songs sung towards the end of bouts were more likely to be cut short than those sung in the beginning.

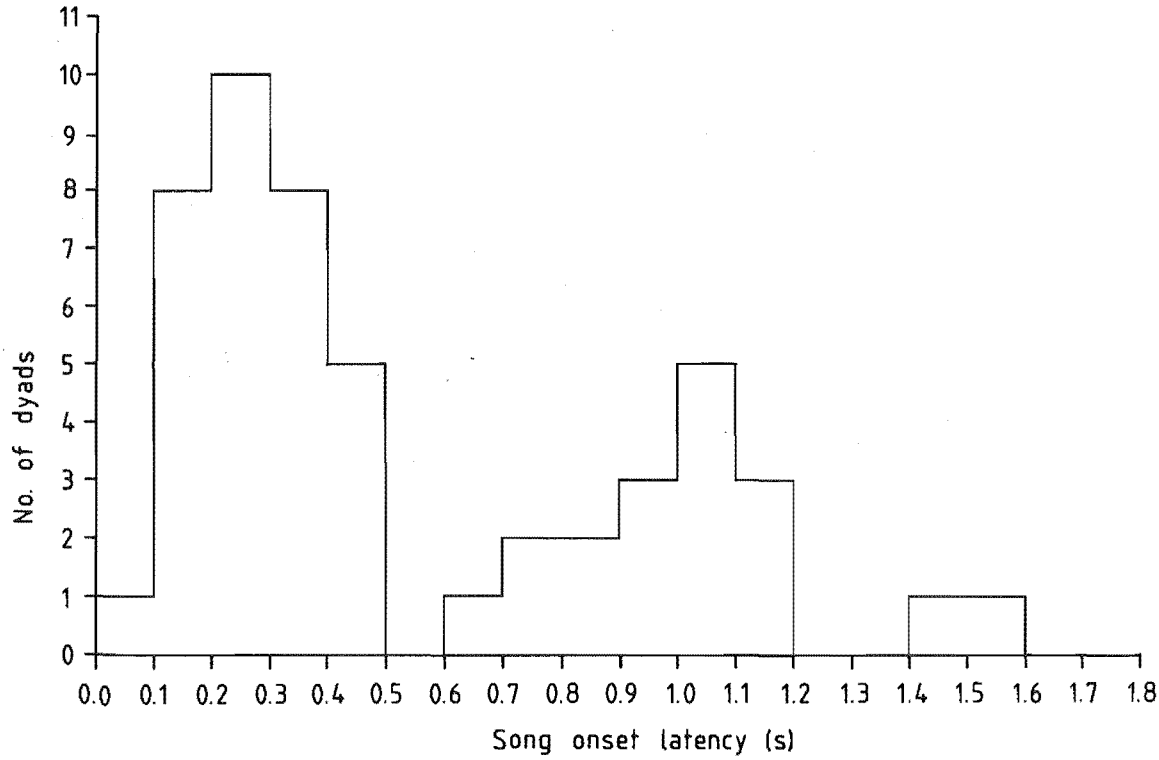

Fig. 10.3. Response delays of 51 randomly selected unison singing dyads (note the bimodal distribution).

Table 10.2 Number of times during a bout that a male assumed the leader role when unison singing.

Participants*					
A	B	A lead	B lead	χ^2	P
M-R	UB-M2	1	11	8.33	<0.005
M-W	M-YR	10	12	0.18	NS
M-WW	MW-YY	9	14	1.09	NS
M-R	M-BG	10	12	0.18	NS
M-R	M-YY	9	11	0.20	NS
M-R	M-W	17	14	0.29	NS
M-BG	M-RB	12	13	0.04	NS
M-WR	UB-M3	10	12	0.18	NS
M-BB	M-RB	16	15	0.03	NS
UB-M4	UB-M5	13	12	0.04	NS

* see page 24 for colour band codes.

Table 10.3 Number of songs truncated by each of the two participants during 10 unison singing bouts.

Participants*		A	B		
A	B	truncates	truncates	X^2	P
M-R	UB-M2	0	10	8.1	<0.005
M-W	M-YR	5	5	0.0	NS
M-WW	MW-YY	4	6	0.1	NS
M-R	M-BG	5	5	0.0	NS
M-R	M-YY	5	6	0.0	NS
M-R	M-W	8	5	0.3	NS
M-BG	M-RB	6	4	0.1	NS
M-WR	UB-M3	4	8	0.8	NS
M-BB	M-RB	7	4	0.4	NS
UB-M4	UB-M5	6	4	0.1	NS

* See page 24 for interpretation of colour-band codes.

In most bouts neither of the contestants showed a preference for truncation (Table 10.3). However, during the dispute between M-R and UB-M2 that took place within M-R's territory, UB-M2 was the only bird to shorten his song. Again, all other bouts took place on territorial boundaries.

Of 67 randomly selected dyads in which one male truncated his song, the bird who did this was always the leader. It should be noted, however, that in three disputes resulting in physical fighting between the contestants, neither of the males shortened his song. These were the only occasions during the study that fighting between males was observed.

SONG SHARING BETWEEN NEIGHBOURS

Both of the transferred males attempted to sing in unison with neighbours who did not share their song patterns. These bouts were shorter in length than those involving males sharing songs ($t=11.07$; $P<0.005$). Unison singing bouts between males that shared songs lasted 12.8 ± 1.9 min ($n=20$), while those involving the transferred

males were only 5.8 ± 1.4 min (n=12).

Unlike males that shared songs with neighbours, the transferred males sang frequently when not unison singing with neighbours. Sampled over a 3-day period, the average number of songs sung, when not vocally interacting with another male, was 8.5 ± 3.0 songs/5 min (n=48) for MR-RB and 4.0 ± 2.7 songs/5 min (n=55) for MR-BB. Local Kowhai Bush males that shared songs with neighbours at the same time of year sang only 0.5 ± 1.7 songs/5 min (n=37).

To determine if this difference in singing rate was a result of a dialect difference (i.e. all Lake Rotorua males sing at a greater rate than Kowhai Bush males), I went to Lake Rotorua at the same time of year and monitored the singing rate there. This rate of 1.1 ± 1.2 songs/5 min (n=20), suggests that the observed differences were not due to populational differences (t-test; $P>0.05$).

Neighbouring males not sharing song patterns frequently trespassed into each other's territories. During a 3-hr period, I observed five intrusions between the territories of MR-RB and his neighbour M-WW and three between the territories of MR-BB and his neighbour MB-WW. During the same week, an average of only one incursion/3 hr was seen between five pairs of neighbours that shared songs.

DISCUSSION

During unison singing bouts male brown creepers adjust their singing performances in at least four ways relative to the singing performances of others. These are discussed below.

VARIATION IN THE NUMBER OF SONGS OVERLAPPED

In several studies, the intensity of a male's response to an intruder or playback song decreases as the intrusion stimulus is moved

away from the centre of the bird's territory (Dhondt 1966, Ickes and Ficken 1970, Falls and Brooks 1975, Catchpole 1977, Wunderle 1978, Melemis and Falls 1982). I found that male brown creepers overlapped more playback songs when these were played in the centre of the territory than when played on the territorial boundary and that no overlapping occurred when playback songs were played outside the territory. The results of this study suggest that the higher the intensity of the interaction and the greater the probability of attack, the more songs the responding bird overlaps. When a male brown creeper reacted strongly to another male he overlapped the song of that male. Thus, the number of songs overlapped may act as a graded signal indicating the intensity of the reaction by the answering male. This assumes that birds know when they are being overlapped, a situation which seems likely (D. Todt, pers. comm.).

ADJUSTMENTS IN THE TIMING OF RESPONSES

A male that responded to the song of another nearby did so rapidly and with temporal overlap. Conversely, males replied more slowly and with little or no overlap to males that were singing several metres away or ones that they were not facing. It has been argued that male nightingales and blackbirds respond rapidly and overlap the songs of rival males who are vocally threatening them (Hultsch and Todt 1982, Todt 1981). A similar argument could be used to explain the rapid and slow responses of male brown creepers to the songs of conspecifics. Nearby males may represent a greater threat to the responding bird than ones further away. A rapid response to the song of a male within close proximity would inform him that his challenge had been met and also indicate that the responding bird was ready to interact further.

INDIVIDUAL PREFERENCES FOR LEADER/FOLLOWER ROLES

During this study males, in most cases, showed no clear-cut preference for being a leader or a follower during vocal interactions. Leader/follower singing has also been examined in both the marsh wren (Cistothorus palustris; Kroodsma 1979) and the red-winged blackbird (Agelaius phoeniceus; Smith and Norman 1979). In these species the social relationship of the interacting males has been correlated with the roles assumed by the males. Kroodsma (1979), while studying the social interactions of two captive marsh wrens, found that the dominant bird (determined by direct attack behaviour) consistently assumed the leader role while the subordinate male took the follower role. Kroodsma argues that the roles assumed provide information about the relative fitness of the two contestants. A different interpretation of leader/follower singing, however, has been proposed by Smith and Norman (1979) after studying the behaviour in the red-winged blackbird. They discovered that resident males were always the followers and intruders, the leaders. If males within their territories are generally dominant over intruding males (Maynard Smith 1979), then in red-winged blackbirds the bird assuming the follower role is the dominant bird. This is just the opposite to the situation reported by Kroodsma (1979).

The lack of role preferences found in this study suggest that a consistent relationship such as dominance/subordinance does not exist between interacting males. This may be due to the fact that most unison singing bouts happened on territorial boundaries where resident/intruder asymmetries probably do not exist. Therefore, in most cases throughout the dispute neither of the males was dominant continuously over the other. However, during one interaction the males did exhibit role preferences. This contest, as mentioned, took place within the territory of one of the participants who was presumably the dominant individual in

the interaction. Here the territory owner assumed the follower role; a pattern similar to that found by Smith and Norman (1979) in the red-winged blackbird.

SONG TRUNCATION

Male brown creepers sometimes truncated their songs during unison singing bouts and this was more apt to occur towards the end of bouts. In addition, both males shortened their songs equally in most bouts; however, the males that truncated were always the vocal leaders in the dyads.

The singing of incomplete songs has been noted in a number of species and may result from the singer's conflict between approaching and escaping (Falls 1969, Ficken and Ficken 1973, Wunderle 1979). Song truncation by brown creepers may also result from such a conflict. Curtailed songs were only noted during unison singing bouts when males were in close proximity, a condition to which they were probably not accustomed. But because only one male at a time truncated his song this explanation seems unlikely.

I propose that males use incomplete songs to indicate their readiness to surrender the contest to the other male. This hypothesis gains support from two observations. First, it may be disadvantageous for individuals to indicate their intentions to yield too early in contests (Maynard Smith 1982b). Brown creeper males were more apt to cut their songs short - which indicated their readiness to surrender - towards the end of a dispute. Secondly, during the three disputes that ended in fighting, both males continued to sing complete songs throughout the contest and neither male gave in to the other.

How might song truncation indicate surrender and overlap singing a threat? First, song in the brown creeper may be important in

territorial defense (Chapt. 6). Furthermore, individual recognition has been demonstrated in the brown creeper and I have suggested that the latter part of males' songs may be a key to this recognition (Chapt. 9). In the European blackbird, which also temporally overlaps songs during social interactions (Todt 1981), the terminal section of the song may also be important in individual identification (Hall-Craggs 1962). Both males' songs are completely masked and their identity hidden when the second male rapidly responds to the first during performance of complete songs. However, when the leader shortens his song, the terminal section of the follower's song is not overlapped and thus revealed. It may be that when a male brown creeper sings and identifies himself at a particular location, he is claiming that location as part of his territory much as mammals do during scent marking.

BARGAINING

Maynard Smith (1979, 1982a, 1982b) has recently suggested that bargaining may be a useful model for understanding the dynamics of communication between interacting territorial males. During bargaining, as in territorial interactions, the resource being contested is divisible and each contestant would like a larger share of the resource than the other is willing to grant yet both would rather share the resource than allow the negotiation to break down and escalate the contest.

The proposed model allows the behaviour of individuals to be described in time and space relative to the position and behaviour of others. Males, can increase their fitness by enlarging their territories from a minimum size or "central area" to a maximum size. Any increase beyond the maximum size, however, does not result in an increase in fitness. Maynard Smith has translated this relationship of territory size and fitness into a measurement of "importance" or the intensity of

defense. "Importance" is highest at the centre of the territory and declines towards the boundary. In such a system, when two contestants display with maximum intensity at the same spot, a breakdown in communication and the bargaining process occurs. During such breakdowns, each contestant has two choices; either to retreat into the central area of the territory and if necessary heighten the contest there or to hold ground and escalate the contest at once.

In contests which involve bargaining, it is probably realistic to assume that each participant possesses incomplete information about the intentions of the other (Maynard Smith 1982b). This is because males are unlikely to have reliable information about the locations of the centres of neighbours' territories. Based on Maynard Smith's model, a male would thus be unable to determine the "importance" of a particular location to a neighbour. With incomplete information available to each contestant, males should begin confrontations with threats of maximum intensity within the bounds of the receiver's gullibility. Bluffing would be the best strategy for both contestants early in the dispute and would result in the transmission of little accurate information about intentions (Wiley 1983).

I propose that the singing adjustments discussed above function in territorial bargaining and help male brown creepers define boundaries. Assuming that each male has determined the location of the centre of his territory, all males should attempt to increase their fitness by enlarging their territories to maximum size as defined by Maynard Smith (1982b).

During the beginning stages of boundary definition, males may sing from a position that defines such a territory of maximum size in what I will call a proposal. If no other bird wants to include that position in his territory no further adjustments are made. However, if a neighbouring male also wants to include this within his boundaries then

he rapidly responds to this initial proposal and the songs of the two birds are overlapped. Thus each male is responding at maximum strength and bluffing the other as far as intentions are concerned.

During the early and middle stages of the interaction each male makes proposals and counterproposals. Towards the end of an interaction the bird assuming the leader role often truncates his song. As I have suggested this indicates his willingness to surrender his claim to the resource being contested. The decision to surrender may be based upon a perception of an asymmetry in the fighting ability of the two contestants (one contestant larger or stronger than the other) or on the length of time the contest has taken relative to the value of the resource. Caryl (1979) has pointed out that although animals tend not to provide reliable information about attack, they do about retreat and surrender. This may explain why contests in which one bird curtailed his song did not involve fighting while in those in which fighting was observed neither contestant truncated his song.

ADAPTIVE VALUE OF SONG SHARING

Neighbouring male brown creepers that interact socially share songs and young birds copy the songs of adult tutors with whom they interact vocally (Chapt. 7). Why do neighbouring males share song patterns? Why is it advantageous for young males to learn the songs of established males?

Payne (1981) has suggested that indigo buntings (Passerina cyanea) which share songs gain an advantage in territorial defense or in attracting a female when they mimic the song of a neighbour. This comes about when young males deceive other conspecifics into mis-identifying them as older individuals whose song they have mimicked. Thus Payne sees young males preferentially learning the songs of older established males.

McGregor and Krebs (1984) have recently shown that great tits shared songs with neighbours but young males did not preferentially copy the songs of established ones. They argued that song sharing between neighbours would be advantageous for reasons other than deceptive mimicry and that song learning from neighbours may arise because neighbours use shared songs in matched countersinging. Thus song sharing is necessary for matching to occur. A number of advantages have been proposed for song matching (reviews: Krebs et al. 1981; Slater 1981) and in the great tit it may be a way of exchanging information about distance (Krebs et al. 1981; Falls et al. 1982).

Based upon the results of this study, I suggest that song sharing between neighbouring male brown creepers allows them to be more efficient in the establishment and maintenance of territorial boundaries. Trainer (1983) has suggested the same for white-crowned sparrows. The complex adjustments in the singing performances of male brown creepers during unison singing bouts may be important in defining boundaries. If males do not sing similar songs and are unable to coordinate their singing then territorial boundaries are not established or at least poorly defined. This could explain the large number of trespasses into the territories of the two transferred males. Furthermore, the two transferred males spent more time singing when patrolling their territories possibly in response to more intrusions. Thus by sharing songs neighbouring males are able to establish and maintain their territorial boundaries efficiently and thereby devote more time and energy to other fitness-increasing activities such as feeding mates or offspring.

CHAPTER 11

SUMMARY

INTRODUCTION

An investigation of the communicatory behaviour of the brown creeper was undertaken. In order to accomplish this it was also necessary to study the species' biology and social organization during the breeding season. Furthermore, to analyse communication during the non-breeding season I had to examine the social organization of wintering birds. The singing behaviour of the brown creeper and its role in intra- and intersexual communication was investigated by examining song variation and the responsiveness of males to this variation. While studying the singing behaviour of males, I discovered an uncommon vocal display which I call unison singing. In this display, interacting males temporally overlapped their songs. I conducted a detailed study of this behaviour in an attempt to understand its functioning in male/male communication and possible role in the definition of territorial boundaries.

The findings from this study are divided into seven parts: breeding ecology, social organization of wintering brown creeper, communicatory behaviour, song learning and variation, responses of males to songs from different localities, neighbour/stranger discrimination and individual recognition, and unison singing in male/male communication.

BREEDING ECOLOGY

The species had a protracted breeding season which could include two complete nesting cycles. The female built the nest in a well concealed spot, usually high in the canopy and laid large eggs, each

making up 18.2% of the female's body weight (11.0 g), in clutches which averaged 3.3 eggs. Incubation lasted ca. 19 days and the nestling period ca. 20 days. At fledging, the young had attained adult size in all characters measured except wing length. After leaving the nest, the young spent 35-65 days with parents. Brown creeper territories covered 0.97 ha. The species formed prolonged year-round pair bonds. The reproductive success of brown creepers was low: hatching was 63.6% while breeding and nestling success were 36.4 and 57.4%, respectively. Predation by introduced mammals was the primary cause of this reduced success. This population had a low annual recruitment rate of 10-12% but the annual adult survival of 80.8% was extremely high.

I suggest that the breeding strategy of the brown creeper is adapted to the mild climatic regime of coastal New Zealand. In these conditions, competition among juveniles for resources, such as food and a breeding site may be extreme. Thus, parents attempt to produce young which have the greatest probability of surviving. Breeding characteristics such as large eggs, small clutches and slow growth rate in young seem to be adaptations to this end.

SOCIAL ORGANIZATION IN THE NON-BREEDING SEASON

During the non-breeding season, members of breeding pairs remained together on their breeding territories defending them from other adults. Juveniles were less site specific and wandered over areas that overlapped the territories of several adult pairs. Nest siblings remained together in flocks during the winter perhaps increasing the young bird's efficiency at finding food through social facilitation or local enhancement. I think that, because brown creepers are often associated with kin, mobbing behaviour in this species may be a result of kin selection.

COMMUNICATORY BEHAVIOUR

The communicatory behaviour of the the brown creeper was studied. I found that the bird's behavioural repertoire consisted of 14 adult vocalizations, 5 nestling or fledgling calls and 7 non-vocal displays. Not all of the vocal displays were discrete; some graded into one another. Most of the vocal signals were used in a broad range of situations which suggests that they encode very general messages and their specificity in communication depends largely on the nature of the recipient and on contextual information. Graded signals may be employed by this species because most interactions occur at close range.

SONG DEVELOPMENT AND VARIATION

Three stages were defined in the development of male song: subsong, plastic song and full song. Young males did not learn their songs from their fathers but from neighbours with whom they vocally interacted. Once the highly stereotyped songs had been learned, males showed little ability to alter them. Neighbours who interacted shared song patterns which resulted in a mosaic of birds singing very similar songs patterns.

Song variation between five populations in the Kaikoura area and three sites on Stewart Island were investigated. The song differences between populations were principally in the morphology of the notes and the general pattern. Of the three models discussed by Payne (1981) to explain the origin and function of song dialects, the historical model best explains the development of the eight dialects studied. The differences in songs between populations may simply be the result of past random events and have no adaptive significance. However, the social adaptation model accounts for the variation of song within populations where subdialects consisted of males that interacted vocally. Males not

interacting had less similar songs. I suggest that these subdialects are a product of song sharing. The adaptive value of song sharing is discussed below in the function of unison singing.

RESPONSES OF MALES TO SONGS FROM DIFFERENT LOCALITIES

Males responses to songs from different dialects were examined by using playback experiments. The males from two populations (Kowhai Bush and Lake Rotorua) were tested with playback songs from three localities (Kowhai Bush, Lake Rotorua and West Bank). Generally males reacted more strongly to songs from their own dialect. However, the Lake Rotorua birds responded equally to their local theme and that of the West Bank. Songs from these two dialects were qualitatively and quantitatively similar. These results suggest that a male's lessened response to foreign songs is caused by the physical dissimilarity between the males own song and the foreign song.

NEIGHBOUR/STRANGER DISCRIMINATION AND INDIVIDUAL RECOGNITION

The ability of male brown creepers to discriminate between the songs of neighbours and strangers and their power to recognize the songs of individuals was investigated by using field playback experiments. Males responded more strongly to stranger's songs than neighbour's. The neighbours of a male in the Kowhai Bush study area who sang the Lake Rotorua theme reacted more vigorously to playback of this male's song than did non-neighbours. These results suggest that associative learning may be involved in neighbour/stranger discrimination. Furthermore, the neighbours of the male singing the Lake Rotorua dialect only weakly responded to the song of another Lake Rotorua male. This demonstrates that males learn specific songs and are capable of individual

recognition. I suggest that the terminal portion of male song is important in this recognition.

UNISON SINGING AND ITS FUNCTION IN TERRITORIAL DEFENSE

During my examination of the brown creeper's singing behaviour, I found that they have a unique form of male/male vocal interaction which I called unison singing. Unlike other forms of vocal interactions the male's songs are temporally overlapped. In order to see if males adjusted their singing performances when interacting with each other and if these adaptations related to the probability that the contestants would behave agonistically towards one another I looked at four possible adjustments: in the number of songs that were overlapped, in the second male's response delay in relate to the first, preferences of males to be either leaders or followers and to truncate their songs during interactions. I also investigated the function of song sharing by studying the vocal interactions that occurred between males not singing the same song patterns. Males overlapped 81.2% of the songs played back to them within their territories, 71.2% when played on territorial boundaries but none when it was played outside the territories. When two males interacted closely (0.5 m) the second male responded rapidly to the first; when further apart (2.4 m) the response was slower. Most males showed no preference to be leaders or followers during unison singing. The bird assuming the leader role truncated his song during most unison singing bouts. In three cases, when the leader did not curtail his song physical fighting developed. I suggest that adjustments are used by males to communicate during the process of bargaining when they are defining their territorial boundaries.

Trespassing into neighbours territories was common between males

not sharing song patterns. I suggest that song sharing in the brown creeper allows males to sing in unison and efficiently establish and maintain territorial boundaries.

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APPENDIX 1

BROWN CREEPER MOBBING BEHAVIOUR

Mobbing was observed both during the breeding and non-breeding season and was only seen when brown creepers were in groups. Mobbing began when one or several group or flock members gave a "rapid" kee in response to the presence of a potential predator. The other flock members responded to this initial alarm by producing the same call and quickly approaching to within 0.5 m of the predator. The birds circled around the predator hopping from perch to perch but always facing the stimulus. While mobbing, the birds' crown as well as throat and breast feathers were erect and their tails were held upright and flicked. If young were close by, the parents often performed the wing-up display. Calling continued as long as the predator was in view and moving but if it remained still or disappeared the initial calling rate diminished quickly and the birds returned to foraging.

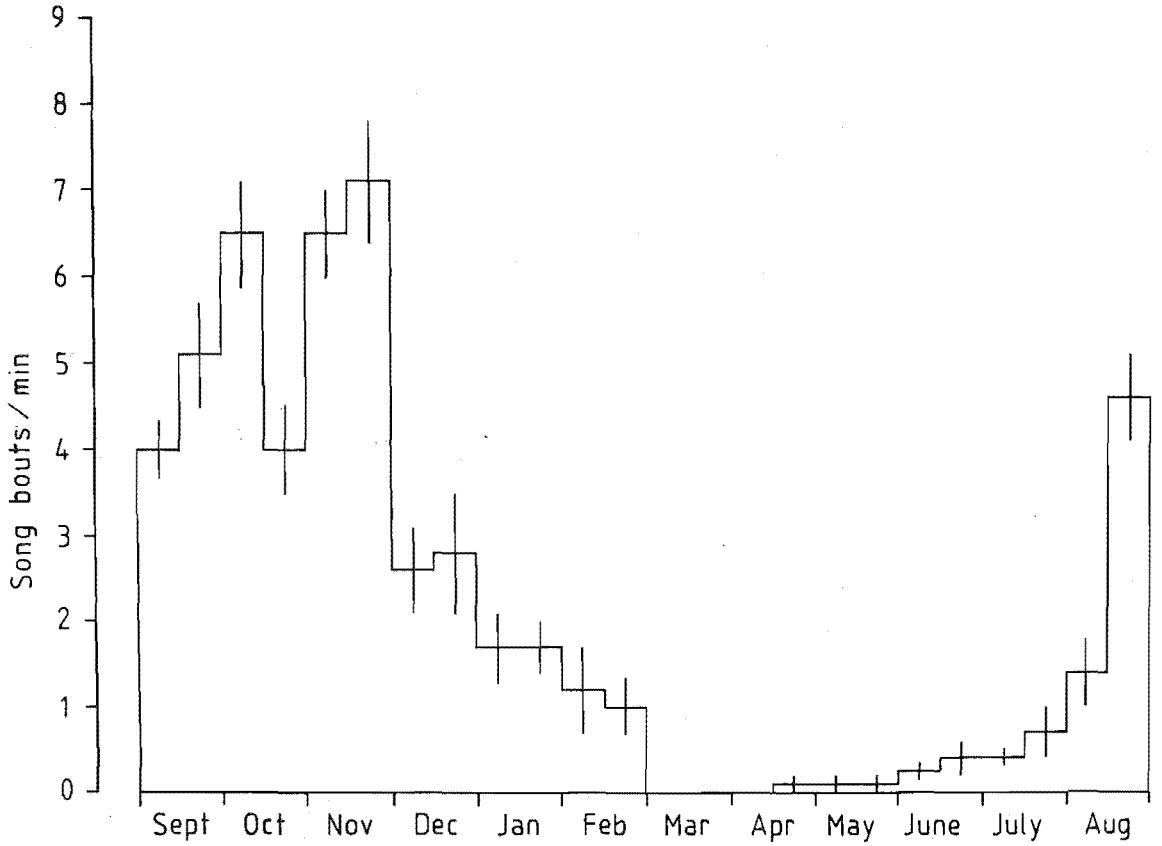
Brown creepers mobbed cats, rats, stoats, kingfishers, shining cuckoos and humans. Frequently, other species such as grey warblers, fantails, silvereyes and bellbirds (Anthornis melanura) responded to the brown creeper's mobbing calls by doing the same. These species also reacted to playback of brown creeper "rapid" kees. It is interesting that the notes of the mobbing call made by the fantail and bellbird are similar in structure to those of the brown creeper (pers. obs.). There may be a selective advantage for each of these species to recognize the mobbing calls of the others. Introduced species such as blackbirds and song thrushes (Turdus philomelos), which are common in Kowhai Bush, however, were never observed to respond to brown creeper mobbing calls.

A total of 57 episodes of mobbing was witnessed in the course of this study. Forty-two of these happened during the non-breeding season

and the remaining 15 took place in the breeding season. All of the mobbings occurring in the breeding season involved parents and their young but during the non-breeding season, in 21 of the episodes, mobbers were either members of sibling groups or aggregates of sibling groups. Flocks composed of adults and their offspring were involved in 18 of the mobbings while the remaining eight were made by flocks consisting of adults and unrelated groups. Thus, during all the observed mobbings kin were present. I found that groups composed only of unrelated birds did not mob.

APPENDIX 2

SEASONAL SINGING ACTIVITY



Appendix 2. Seasonal variation in the number of song bouts heard per month. Months are divided into two equal periods.

APPENDIX 3

HISTORY OF THE TERM "UNISON SINGING"

The term "unison singing" as used herein refers to a unique form of overlap singing by males that occurred during territorial interactions. This expression should not be confused with that used by some authors to describe a type of duetting in which the two members of a mated pair give the same vocalization simultaneously (Armstrong 1963, Thorpe 1972, Short and Horne 1983). Hultsch (1983) used the phrase "unisono singing" to describe a male/male vocal interaction in male Heuglins robin chats (Cossypha heuglini) that is superficially similar to what I have found in brown creepers. However, the term unisono singing has also been applied to male/female duetting in which both sexes sing the same song simultaneously (Wickler and Seibt 1980). Thus, one must be certain as to whether the author is referring to male/female duetting or male/male singing when the term unison or unisono singing is used.